VARIATION IN THE EFFECTS OF DISTURBANCE ALONG A SOIL DRAINAGE GRADIENT FOR A LOWLAND TEMPERATE RAINFOREST SOUTH WESTLAND NEW ZEALAND

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Abstract

Variation in the effects of disturbance across three differently aged glacial terraces in a terrace rimu (*Dacrydium cupressinum*) forest were investigated. Disturbance histories were reconstructed and associated patterns of stand development, differences in stand composition and stand structure determined. This forest variation was related to environmental variation between the differently aged terraces.

Forest stand composition was investigated across the three terraces using Indicator Species Analysis and Detrended Correspondence Analysis for data collected from ninety stands. This data was used to categorise forest community composition. Analysis of stand structure focused on the dominant stand type on each of the three terraces for which disturbance histories and patterns of stand development were determined. Disturbance histories were reconstructed form size and age-class frequency distributions, and the spatial distribution of tree ages to identify even-aged groups of trees that had established in response to past disturbance. Soil drainage and stage of soil development were determined for the dominant stands.

Differences in stand structure between the three main stands reflected differences in disturbance history which were associated with different soil profile and soil drainage characteristics. For stand S1 on the oldest terrace the spatial distribution of tree ages showed that catastrophic disturbance had occurred on the most poorly drained and deepest soils. For stand S2 on the middle aged terrace sporadic gap formation had occurred on less poorly drained and shallower soils. For stand S3 on the youngest terrace progressive canopy mortality had occurred on the shallowest soils, of a similar drainage to those in stand S2. Variation in the soil characteristics between terraces reflected a secular trend in soil development towards increased depth and poorer drainage.

Stand composition was primarily influenced by disturbance history. The effects of different

disturbance histories on stand composition was inferred from species regeneration patterns, the distribution of seedlings beneath different canopy cover classes, and gap regeneration characteristics. The least shade tolerant species, *Dacrydium cupressinum*, *Lagarostrobos colensoi* and *Phyllocladus alpinus* favoured regeneration after infrequent catastrophic disturbance. While the more shade tolerant *Prumnopitys ferruginea*, *Weinmannia racemosa* and *Quintinia acutifolia* favoured establishment following more frequent canopy gap formation.

Differences in stand composition also reflected differences in soil drainage, interspecific competition, and stand structure. The association of species with differently drained soils within stands and between stands suggested *Lagarostrobos colensoi* and *Phyllocladus alpinus* favoured the most poorly drained soils, while *Prumnopitys ferruginea* favoured less poorly drained soils. Interspecific competition accounted for ongoing compositional changes where *Dacrydium cupressinum* appeared to be competing out *Phyllocladus alpinus* and *Lagarostrobos colensoi* on account of its greater stature and longevity. Stand structure affected species richness. The least number of species was associated with the most uniform stands while the highest number of species was associated with the least uniform stands. Uniform stands were presumed to reduce the chance of colonisation by differentially adapted species.

Variation in the effects of disturbance explained changes in stand structure and composition across the terraces. A secular change in the stand dynamics of terrace rimu forest is envisaged over millennia reflecting soil development, where changes in forest composition and stand structure reflect the interaction of disturbance and soil drainage.

Chapter 1

Introduction

Forest vegetation exhibits pattern, reflecting both variation in structure and composition that occurs along a continuum of temporal and spatial scales. This thesis examines changes in both temporal and spatial aspects of forest pattern to determine the main factors causing forest change across a lowland *Dacrydium cupressinum* dominated terrace forest. The study focuses on middle to long term temporal change, and small to intermediate scale spatial change. Middle to long term temporal change reflects successional mechanisms and patch dynamics processes that operate over decades to hundreds of years, and changes that occur over millennia that result from equally long term environmental change (Veblen 1992). Small to intermediate scale spatial change reflects changes that occur from individual species replacement by another species to changes at the size of disturbance openings created by catastrophic disturbances (100's of hectares). In this chapter concepts of vegetation change that can account for these different temporal and spatial scales of forest pattern are reviewed.

1.1 The successional viewpoint

Early views on vegetation change focused on explaining the temporal pattern of species replacement, suggesting mechanisms of change that emphasised properties of the plant (autogenic mechanisms). Up until the 1970's the theoretical framework for vegetation change relied heavily on Clement's (1916) successional view point (Glenn-Lewin & Maarel 1992). Clement's successional theory explained compositional changes and was an equilibrium model assuming that vegetation change progressed until the stable vegetation type (the climax community) was in equilibrium with the regional climate and site (Drury & Nisbet 1973). The theory emphasised that the development of the climax community was orderly and predictable and occurred in long disturbance free periods (Glenn-Lewin & Maarel 1992). The mechanism was dependant on the process of competitive exclusion (Pickett

1980) where two species cannot coexist in the same niche (Whittaker 1975), otherwise known as Gause's principle.

The underlying mechanisms of vegetation change, are to be found in the population processes of the constituent plant species. There are two main ways in which vegetation influences species replacement, through the effect of one species on another and through environmental modification (Glenn-Lewin & Maarel 1992). A variety of mechanisms have been proposed incorporating these two ideas.

The presence of residual propagules and subsequent vegetation development following a disturbance are important for Egler's (1954) initial floristic composition and relay floristics models. The plants present from the beginning pre-empt the growing space preventing new colonisers, with development proceeding as groups of plants modify the growing environment and die out. This is followed by an increased dominance of new groups of plants that were present from the start, but are more suited to the new environment.

Drury & Nisbet (1973) recognised the significance of life histories of plants. They suggested that short life cycles, differences in height growth rate, long seed viability and chemical defenses against herbivory were important determinants of vegetation change. Life histories were the key to Noble & Slatyer's (1980) vital attributes model. This model was based on a small number of highly significant life history traits e.g., age at first reproduction, longevity or life span, and propagule persistence. It predicted the sequence of vegetation development in communities exposed to recurrent disturbances. There are similarities between this model and Bazzaz's (1979) model that emphasised the importance of different physiological attributes between early and late successional species.

Connell & Slatyer (1977) focused on species interactions as a mechanism of vegetation change, and summarised species interactions during succession into three different processes.

1. The facilitation model. The entry or growth of the late successional species is dependant upon the earlier species providing favourable environmental change for the future species, e.g., soil development.

2. The tolerance model. A predictable sequence of vegetation change is produced by the existence of species that have evolved different strategies for exploiting resources. Later species will be those able to tolerate different levels of resources to the earlier ones.

3. The inhibition model. All species resist invasion of competitors. The first occupant(s) pre-empts the space and will continue to exclude or inhibit later colonists until the former die or are damaged, thus releasing resources.

These processes focus on the sequential replacement of species as succession progresses. However successional theory predicts that once the climax vegetation type has been reached the community is self perpetuating. Fox (1977) explained this in terms of his alteration and coexistence of species model. Local regulation of species composition occurs because dominant trees modify biotic and abiotic factors differentially according to the species, providing a microhabitat for younger or smaller plants. This influences the probability that a species will be replaced after its death by another species. The model emphasises autogenic habitat heterogeneity.

Successional mechanisms can also account for spatial vegetation change at small to intermediate scales. The presence of vegetation at different stages of succession creates spatial discontinuities in composition and structure. In addition, habitat modification by different species creates different opportunities for colonisation which can also account for spatial change. However, compositional changes commonly reflect the distribution of plants along environmental gradients, often reflecting a complex of topographic, climatic and edaphic factors. These create spatial gradients in the plant habitat such that the distribution of species along the gradient reflects their differential adaptations

(Whittaker 1975). Such spatial changes can occur in conjunction with temporal change when long term (millennia) changes occur in the environment, e.g., climatic change or soil development.

1.2 The Patch Dynamics view point

The above theories focused on autogenic factors associated with vegetation change. However, contemporary views emphasise the importance of allogenic factors (change attributed to factors external to the community) from repeated disturbances to which survivors of disturbance or new colonists respond. Early workers observed the effects of disturbance from observations of regeneration in forest gaps (Aubreville 1938; Watt 1947; Richards 1952). Watt (1947) suggested that fine scale gap dynamics controlled the spatial and temporal distribution of regeneration in a mesic temperate forest creating a mosaic of gap, building and mature phases that constitute the forest growth cycle (Whitmore 1988). The effects of disturbance relate to the release of space related resources which create differential opportunities for establishment and growth (Veblen 1992).

The role of disturbance in plant communities is recognised using the concept of patch or gap dynamics. Patch dynamics refers to the pattern of patch creation in time and space, patch size and structure and the change in individual patches of a cohort and size class due to species availability, adaptations, and interactions (Pickett & White 1985).

Disturbances range on a continuum from entirely endogenous (disturbances caused by internal factors e.g. tree senescence) to entirely exogenous (disturbances generated by external factors e.g., wind), but are unlikely to occur in isolation. For many types of disturbance there is a gradient from minor to major effects, e.g. wind affects forests on a scale from the pruning of branches to windthrow of standing dead trees to extensive blowdowns caused by hurricanes and gales (White 1979; Spies & Franklin 1989). The classical exogenous disturbance acts at a point in time, creates abrupt boundaries and increases resource availability through decreased resource use or increased decomposition.

How a particular disturbance event will affect the distribution of resource and the distribution and coexistence of species in an area will be influenced by the nature of the landscape (Pickett & White 1985). Disturbances vary regionally and within one landscape as a function of topography and other site variables (e.g. aspect and soil drainage) (White 1979) . Hence different topographic positions may have very different disturbance regimes, characterised by their predictability, frequency and magnitude (Shugart & Seagle 1985). It is this disturbance regime that determines species interactions and coexistence (Armstrong 1976).

1.3 Species Coexistence

Explanations of species coexistence in plant communities at or near compositional equilibrium rely on resource partitioning, life history differentiation or disruption of biological interaction by fine scale disturbances, or a combination of all three (Veblen 1992). Explanations based on resource partitioning rely on the presence of species with different niches (Pickett 1980). However this is not a good explanation for species of the same life form and phenological behaviour in a uniform habitat (Veblen 1992). An alternative explanation of species coexistence is the non equilibrium view point (Pickett 1980) where disturbances occur with a high enough frequency to destroy or disadvantage the competitive dominance of late successional species and so allow the coexistence of species with varying degrees of competitive ability (Armesto & Pickett 1985). In such communities compositional equilibrium is never attained (Veblen 1992).

Connell (1979) suggested intermediate levels of disturbance will maximise species diversity, causing an optimum level of disruption of biological interactions without being so severe as to cause local species extinction. However Collins & Barber (1985) proposed a modification of the theory that reflects the effects of different concurrent disturbance events. Effects of different disturbances were two fold, limiting the ability of a small number of species to achieve competitive dominance, and increasing habitat heterogeneity. This model emphasised the interactions of natural disturbances and their independent effects.

Grubb's (1977) concept of "the regeneration niche" (an expression of the requirements for a high chance of success of the replacement of one mature individual by another mature individual of the next generation) explained species coexistence based on differences in the regeneration requirements of species. This model of species coexistence is consistent with the theory of resource partitioning and environmental heterogeneity induced by fine scale disturbances (Veblen 1992). Gradients in disturbance can result in niche separation of the species involved in gap dynamics (White 1979) through modification of microsites and indirectly by altering plant influences on microsites. Niche separation due to gap dynamics may complement or contradict niche separation associated with environmental gradients. A particular disturbance regime may allow expansion across the coencline (changes in the population of plants associated with the environmental gradient) (White 1979). Hence the relative effects of the complex environmental gradient and the disturbance gradient will be difficult to separate.

Coexistence may also be explained by differences in life history strategies e.g.,Swaine (1989) found the population of tree species in a west African tropical forest to be maintained by different turnover rates due to contrasting death and recruitment rates.

Hence contemporary views of vegetation change reflect both plant induced changes, the distribution of species along environmental gradients, and the effect of intermittent exogenous disturbance.

1.4 Forest Dynamics

Forest dynamics is the study of changes in forest stand structure with time (stand development), including stand behaviour during and after disturbance (Oliver & Larson 1990). A stand is a spatially continuous group of trees and associated vegetation having similar structure and growing under similar soil and climatic conditions.

The dynamic nature of forests led Aubreville (1938) to put forward the mosaic or cyclic theory of

regeneration for tropical forests, suggesting that a given area of forest consists of a space time mosaic of different combinations of different species. Richards (1952) extended the theory, indicating the importance of gaps and the interaction with differences in shade tolerance and other life history characteristics of different species.

The importance of gaps has been a central theme in the development of hypotheses on forest regeneration mechanisms (e.g. Whitmore 1989). There are two major patterns of gap response:

1. The reorganisation response, which involves the release of plants established prior to the disturbance and the subsequent competition that results in a replacement individual.

2. The new establishment response, which results in the establishment of new plants within the area of disturbance (Ehrenfeld 1980). For this type of response gap size has been viewed as the main factor determining which species will regenerate (Canham 1989).

Species response to different sized disturbances varies between two extreme end points, from trees that will persist in the shade to those that grow in the open resulting in a tree by tree replacement system (Canham 1989). The regeneration behaviour of species has been characterised in relation to the scale of disturbance (gap size) (Veblen & Stewart 1980; Veblen 1992). A continuum of regeneration modes may be arbitrarily segregated into catastrophic, gap-phase and continuous modes (Veblen 1992).

1. Catastrophic regeneration refers to the establishment of most of a population during a short time in large openings (canopy gaps) formed by infrequent massive disturbances such as flooding, mass movement or windthrow (Ogden & Stewart 1995). Large discontinuities in age structure and large patch sizes (> 1000m^2) reflect this form of regeneration which is typical of shade intolerant species (Veblen & Stewart 1980).

2. Gap-phase regeneration refers to regeneration in smaller gaps (<1000m^2) such as those resulting from the death of one to several trees. Smaller patch size and fewer age discontinuities could indicate gap-phase regeneration.

3. Continuous regeneration refers to the attainment of maturity in the absence of a disturbance caused canopy opening and would result from the growth of seedlings and saplings beneath forest canopies so that there is a continuous replacement of older dying canopy trees. An exponential decline in tree numbers with increasing diameter is the classic expression of a continuously regenerating stand.

Many studies of forest dynamics have focused on characterising age and size-class frequency distributions that reflect both species regeneration mechanisms and different scales, frequencies and types of disturbance (reviewed in Lorimer 1985). Age distributions have often been inferred from size distributions, on the basis that age and diameter are correlated (Lorimer 1985). However age is often a poor indicator of diameter because of variability in growth rates caused by differences in stand structure, environment and life histories (Stewart 1986). Improved relationships are often obtained from species growing in all-aged stands and from shade tolerant species. Shade tolerant species can often grow in shaded and well lit environments maintaining a consistent diameter increment.

Even when good age-diameter data is available the results can be misleading. e.g., the presence of even-aged groups of trees is often used as compelling evidence of past disturbance (Duncan & Stewart 1991). However, a disturbance that kills overstory trees but leaves most of the understory intact is often followed by a broadly uneven-aged stand (Lorimer 1985).

Temporal and spatial variation of disturbance events affect forests in different ways. Differences in the disturbance regime affect stand structure and change the proportion of shade tolerant and shade intolerant species. Whitmore (1989) suggests that where large gaps are replaced by smaller ones

there is a shift from shade tolerant climax species to light demanding pioneer species.

Shade tolerant species may respond to even slight increases in understorey light levels produced by the penetration of diffuse radiation through small openings anywhere in the canopy. This together with the ability to withstand periods of suppression when no gaps are present nearby allows shade tolerant species to exploit disturbances that create numerous ephemeral openings. Thus the fate of individual saplings of shade tolerant species can depend on the frequency of disturbance and the duration of periods of release versus suppression more strongly than on gap formation *per se* (Canham 1989).

Although size and frequency of canopy gap formation is important in determining stand structure and composition, different stand structures can reflect the differential response of species to different types and intensities of disturbance (reflecting disturbance history) even though frequency and scale of gap formation are similar (Runkle 1985). Intense fire in North America can result in dense stands of *Pinus contorta*. Fire is required for the opening of serotinous cones and results in profuse regeneration. However, less intense partial burns result in less abundant regeneration of *P.contorta* favouring less fire resistant species (Muir 1993). Large blowdowns can simply result in the accelerated growth of subcanopy trees or the sprouting of damaged trees, while more intense windstorms result in new regeneration (Veblen et al 1989). Differences in composition between stands can also result from differences in resistance to disturbance between species, e.g., blowdowns can shift dominance towards windfirm species (Veblen & Lorenz 1987).

The change in structure and composition of post-gap vegetation is intimately linked with the stand structure at the time of disturbance (reflecting disturbance history), seedling regeneration, position in the landscape (e.g. topographic location) and the availability of potential colonists. Differences in disturbance history provide different opportunities for regeneration of tree species by influencing the extent of competing understorey vegetation and by influencing the availability of different

establishment sites (Stewart et al 1991). Duncan (1993) found variation in the intensity of disturbance affected the proportions of different establishment substrates available and hence the proportion of differentially adapted species represented in the forest. However, this is not an exclusive rule since Brown & Press (1992) found that the size of seedlings at the time of gap creation was most important in determining which species dominated gaps in a dipterocarp forest in Malaysia. This occurred irrespective of shade tolerance and species growth rates.

1.5 Forest dynamics of Southern Hemisphere conifers

Genera of southern hemisphere conifers occur extensively in the temperate rainforests of New Zealand, Tasmania, and South America, and are scattered in the tropical rainforests of Melanesia, South Africa, South America and northeast Australia. Individual trees often occur as conspicuous emergents, (20-40m) taller than the tallest associated angiosperm trees (Whitmore 1975). In the forests of New Zealand the conspicuous emergent conifers include species of *Agathis*, *Dacrydium*, *Podocarpus*, *Dacrycarpus*, *Prumnopitys* and *Libocedrus* (Veblen & Stewart 1982) and are characteristically long lived. e.g. maximum ages of: *Libocedrus bidwillii*, 744 years (Stewart & Rose 1989), *Dacrydium cupressinum* 1160 years, and *Prumnopitys ferruginea* 771 years (Lusk & Ogden 1992) have been recorded. Early views explained the occurrence and composition of the southern hemisphere coniferous forests based on the successional paradigm. Frequent studies have commented upon the paucity of seedlings and saplings of the conifer species which was viewed as strong supporting evidence for their successional status.

Cockayne (1928), viewed the conifers in New Zealand as seral light demanding species that were being eliminated by the more vigorous shade tolerant angiosperms. In the South Island of New Zealand kamahi (*Weinmannia racemosa*) was considered to be the climax species. Similar views were postulated for *Agathis macrophylla* in the Solomon Islands (Whitmore 1966), *Araucaria* species in New Guinea (Womersley 1958) and for *Araucaria araucana* in Chile (Scmithusen 1960). Robbins (1962) regarded the conifers as relicts. As a consequence, stands of conifers were viewed as an

outcome of a past catastrophe that had removed the angiosperm competition (e.g Womersley 1958; Aubreville 1965; Whitmore 1966) and in some cases their presence reflected relegation to poor quality soils (e.g. Webb & Tracey 1967; Midgley & Bond 1989).

Climatic change was postulated as an alternative hypothesis to explain the lack of regeneration of the conifers. In New Zealand, Holloway (1954) suggested the paucity of conifer regeneration was caused by recent climatic change towards a cooler and drier climate starting in the thirteenth century. Similar ideas were postulated for forests with a coniferous element in South America (Kalela 1941 reviewed in Veblen & Lorenz 1987), and also a general drying of the climate was considered important for regeneration failure of mistbelt podocarp forests in Natal, South Africa (Moll 1972).

The above ideas largely ignored some of the prior studies that suggested that disturbance was an important determinant of regeneration and stand structure (e.g Hutchinson 1932; Poole 1937; Cameron 1954). Cameron's (1954) mechanism involved a cyclic succession of dominants where conifers alternated with angiosperms on an individual site resulting in a mosaic of patches at different stages of development. This theory accounted for the poor representation of canopy dominants in the understorey.

In line with contemporary thinking, exogenous disturbance is now considered important for determining the structure and composition of southern hemisphere coniferous forests. Disturbance regimes in southern hemisphere coniferous forests vary from small scale and frequent tree falls (Geldenhuys & Maliepaard 1983) to large scale infrequent catastrophic disturbance events caused by flooding (Duncan 1993), fire (Veblen & Lorenz 1987), hurricane and mass movement (Veblen et al 1980; Stewart & Rose 1989) and vulcanism (Veblen 1982).

In addition to the effects of different scales and frequencies of disturbance a species may also display different modes of regeneration depending on the forest community in which it is growing. e.g., shade

intolerant species normally require sizeable gaps in the canopy for successful establishment, however small gap-phase and continuous regeneration may occur when the forest is reduced in stature or a deciduous component is present promoting higher light levels than would occur in a typical conifer-angiosperm forest; e.g., *Athrotaxis selaginoides* and *Phyllocladus asplenifolius* in Tasmania regenerate continuously in open communities (Read & Hill 1988), but discontinuously in scrub rainforest on poor soils in which canopy gaps are small and quickly occupied by species that reproduce vegetatively. In New Zealand, gap-phase regeneration of *Libocedrus bidwillii* occurs when poor drainage reduces the abundance and vigour of most other tree species establishing in gaps (Veblen & Stewart 1982). However in closed communities, infrequent but catastrophic events maintain the establishment of viable populations of *Libocedrus* (Veblen & Stewart 1982; Stewart & Rose 1989).

Similar forest communities may be exposed to different types of disturbances affecting their structure and composition, e.g., catastrophically regenerated stands may be followed by secondary smaller disturbances resulting in a gap phase regeneration (e.g. Veblen & Stewart 1982; Ogden et al. 1987; Ogden & Stewart 1995). For *Austrocedrus chilensis* and *Nothofagus dombeyi* forest in Chile, fire and blowdowns are important factors controlling stand structure and competition (Veblen & Lorenz 1987). Blowdowns shift the dominance towards *A.chilensis* due to its windfirm nature while in even aged old-growth stands unaffected by fire and windthrow, gap replacement results in sporadic recruitment with all-aged distributions of both species (Veblen 1988).

The ability to vegetatively regenerate is also an important regeneration strategies for some species. Veblen (1982) found root suckering to be important for *Araucaria araucana*. At its upper limit the frequent exposure of roots caused extensive root suckering resulting in the formation of pure stands. For shade tolerant *Saxegothea conspicua* in Chile regeneration occurs mainly by means of adventitious roots and occasional basal sprouting (Veblen 1980).

The studies reviewed show that contemporary work on the stand dynamics of southern hemisphere coniferous forests has focused on the characteristics and effects of different disturbance regimes/disturbance histories. The importance of disturbance for determining stand structure and for the regulation of species composition and coexistence has been documented.

1.6 Study background and objectives

In New Zealand, studies have emphasised the necessity of disturbance for forest regeneration on different landforms from montane to lowland forest communities, characterising different disturbance histories from flooding, windthrow, mass movement and vulcanism. Different patterns of stand development have been attributed to different scales of disturbance (e.g. Veblen & Stewart 1980).

In Westland, variation in stand structure and composition reflects both the distribution of species along environmental gradients, such as stage of soil development and soil drainage (Stewart & Harrison 1987), and the effect of different disturbance histories (Duncan 1993). Early qualitative studies on the stand dynamics of terrace rimu (*Dacrydium cupressinum*) forest suggested windthrow formed variable sized patches from 1 to 200ha (Hutchinson 1932). Over the last decade more quantitative studies have shown that *Dacrydium cupressinum* regenerates in even-aged groups on glacial terraces, suggesting that the terrace forest is a mosaic of differently sized and differently aged groups (Six Dijkstra et al. 1985; Cornere 1992), reflecting variation in the disturbance pattern.

While there are obvious differences in vegetation pattern between hill and terrace forest (Chavasse 1954; Simmons 1982; Norton 1994) there also appear to be differences in forest structure on the same landform. Studies suggest that differences in stand structure on the terrace forest may be attributed to the combined effect of disturbance and soil drainage, (Cornere 1992).

Many studies have documented the influence of environmental gradients on structure and composition, while little attention has been given to the influence of differences in disturbance on

similar landforms within the same general forest type. The objective of this study is to examine variation in the effects of disturbance on stand composition and structure along environmental gradients. It is hypothesised that forest variation (changes in stand structure and composition) associated with differently aged glacial terraces of a lowland terrace rimu forest reflects variation in the effects of the dominant disturbance type (presumed to be windstorms) along a soil drainage gradient.

This study examines differences in disturbance history, changes in stand structure and patterns of stand development (including species composition) that occur on three differently-aged terrace landforms in Saltwater Forest. Forest stand composition is investigated within and between terraces using Indicator Species Analysis and Detrended Correspondence Analysis. Patterns of vegetation change are investigated for the dominant stand structures on each terrace from detailed stand analysis and from stand disturbance history reconstruction. Age and size-class frequency distributions, and stem spatial locations are used to identify even-aged patches of trees that established in response to past disturbance. The spatial location of trees is used in conjunction with data from gap surveys to reconstruct gap replacement and stand development sequences. In addition data is presented on environmental variation reflecting stage of soil development and soil drainage for different stand structures.

To address the above hypothesis I addressed the following questions:

1. Does stand composition vary across the terraces?
2. Does stand structure (diameter, stem density and basal area) vary across the terraces?
3. What is the diameter, age and spatial structure of the dominant stand type on each terrace?
4. What are the regeneration patterns of the main tree species for the different stand structures?
5. What are the disturbance histories and patterns of stand development for each of the dominant stands?
6. What effect do the different disturbance histories have on seedling and sapling establishment patterns?
7. What are the main disturbance and environmental factors affecting forest composition?
8. What factors cause variation in the effects of disturbance?
9. What other factors may account for forest variation across the terraces?
10. What is the combined influence of disturbance and soil drainage on the stand dynamics of terrace rimu forest?

Chapter 2

Study Area

2.1 Location

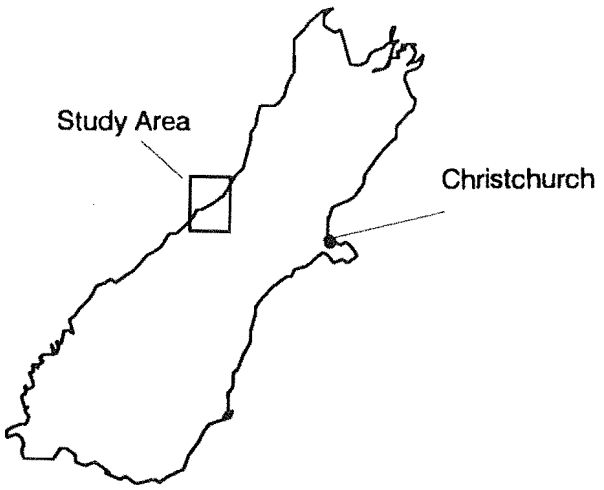
This study was carried out in Saltwater Forest on the West Coast of New Zealand's South Island. The study sites were situated at approximately latitude 43°08'S, longitude 170°25'E, ten kilometres to the west of HariHari (Figure 2.1) in the Whataroa Ecological Region and the HariHari Ecological District. Salltwater Forest lies between the Saltwater Ecological Area and the Southern Alps (12km to the southeast), and is bounded by two rivers; the Poerua to the north/northeast and the Whataroa to the south/southwest. The study sites were located across the forest on three differently aged glacial terrace surfaces as identified by Almond (in press). The forest type investigated had also been studied by Six Dijkstra et al. (1985) and Cornere (1992) and is considered typical of lowland terrace rimu (*Dacrydium cupressinum*) forest in south Westland.

2.2 Vegetation in south Westland

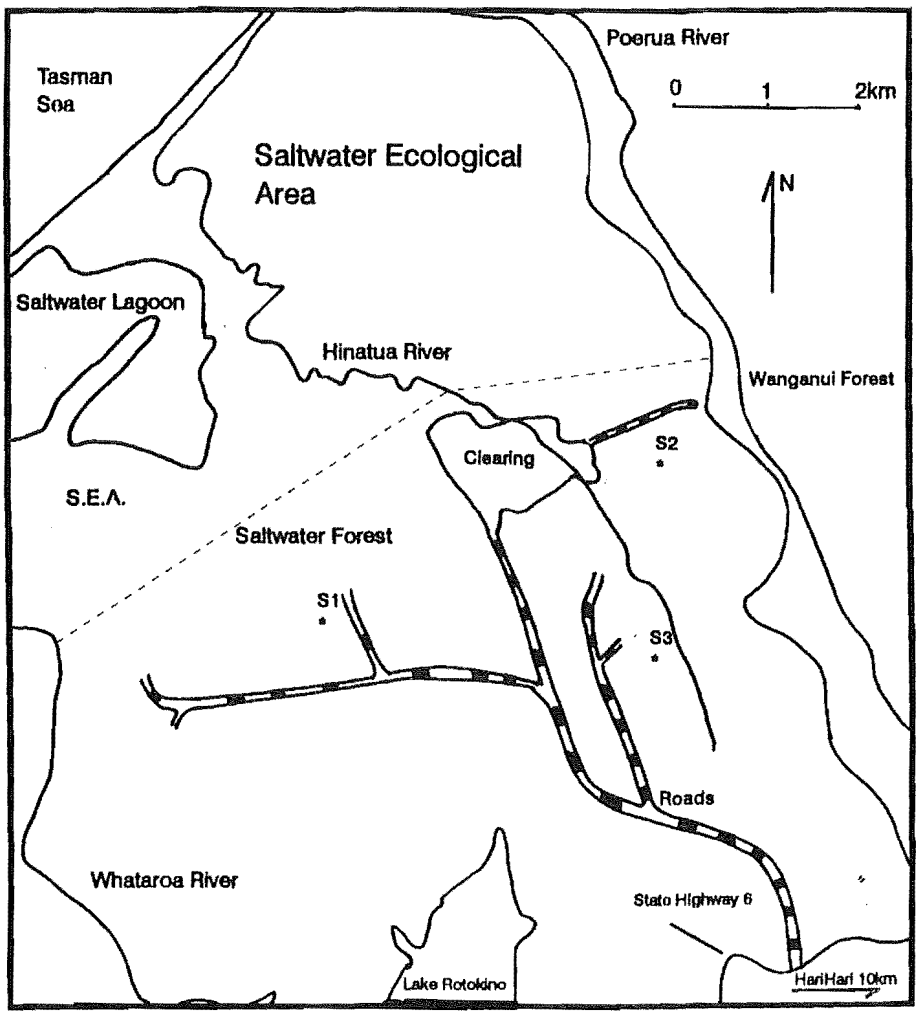
The piedmont west of the Alpine fault and the lower slopes of the Southern Alps are clothed in dense mixed forest that varies from rata/kamahi forest or beech forest (*Nothofagus* spp) on the lower slopes (100-700m) to dense stands of tall conifers in the lowlands. Beech forest is replaced by mixed forest in Westland between latitudes 42° 40' and 43° 40' (the "beech gap") (Wardle 1991). Recent alluvial soils are mostly cleared to pasture, and outwash terraces in the north have been logged and burnt, but in south Westland extensive areas of conifer/angiosperm forest remain. These forests vary along catenas of drainage and fertility associated with different landforms. A close relationship has been shown between landform, soil and vegetation pattern in Westland (Chavasse 1971; Smith & Lee 1984; Sowden 1986; Basher 1986; Stewart & Harrison 1987; Norton & Leathwick 1990; Duncan et al. 1990; Norton 1994).

Figure 2.1: (a), Location of the study area, Saltwater Forest, south Westland in relation to South Island of New Zealand, and (b), the location of the three main study plots S1 (terrace 1), S2 (terrace 2) and S3 (terrace 3) within Saltwater Forest.

(a)



(b)



The low altitude tall forest (below 400m) has been broadly classified between forests that occur on mature soils on the fluvioglacial terraces, and those that occur on recent alluvial surfaces, and has been comprehensively described by Wardle (1977). On the flats and terraces dense conifer forests occur. Podocarps form the main canopy at over 30m above a subcanopy of angiosperms. A *Dacrycarpus dacrydiodes* community occurs on recent poorly drained sites, and on silty soils. *Dacrycarpus* is the physiognomic dominant reaching a height of 50m, coexisting with variable proportions of *Dacrydium cupressinum*, *Prumnopitys taxifolia* and *Prumnopitys ferruginea*. Better drained soils than those with dense *Dacrycarpus dacrydiodes* support a mixture of conifers, although most stands on such sites have been modified by logging. *Prumnopitys taxifolia* is dominant on silty soils and *Podocarpus totora* on stonier ground. On alluvial and fluvio-glacial terraces where soil drainage is poor a *Dacrydium cupressinum* community dominates and may be codominant with *Lagarostrobos colensoi* where drainage is extremely poor. *Prumnopitys ferruginea*, *Phyllocladus alpinus* and *Podocarpus hallii* also occur, but are generally less abundant. Where the topography changes to rolling hills such as on the moraines adjacent to the fluvio-glacial terraces conifer/angiosperm forest occurs. The main canopy is formed by angiosperms, but conifers are present usually as a discontinuous overstorey of wide-crowned trees with large boles. The forest type investigated in this study is the *Dacrydium cupressinum* community that occurs on the fluvio-glacial terraces.

2.3 Vegetation description

Dacrydium cupressinum (rimu) is the dominant species of the lowland terrace forest, and stands are often described on the basis of the *Dacrydium* element (Six Dijikstra et al. 1985; McKelvey 1985). However *Lagarostrobos colensoi* (silver pine) and *Prumnopitys ferruginea* (miro) may be locally dominant (e.g. Cornere 1992). *Phyllocladus alpinus* (mountain toatoa) is also common but is generally scattered through the forest. Other conifers, such as *Dacrycarpus dacrydiodes* (kahikatea) and *Prumnopitys taxifolia* (matai) occur as rare tall stems. *Prumnopitys ferruginea* and *Lagarostrobos* are generally shorter in stature than *Dacrydium*, and are usually found in the subcanopy and understorey although in some instances *Lagarostrobos* can be co-dominant with *Dacrydium* in the

canopy. *Phyllocladus* is generally confined to the understorey with occasional stems in the sub canopy. The angiosperms *Weinmannia racemosa* and *Quintinia acutifolia* are generally common in the understorey and often dominate the sub canopy (Wardle 1991).

Other common understorey species include *Neomyrtus pedunculata*, *Elaeocarpus hookerianus* (pokaka), *Pseudopanax crassifolius* (lancewood), *Griselinia littoralis* (broadleaf), *Pseudopanax colensoi* (three-finger), *Myrsine australis* (red matipo), *Coprosma foetidissima* (stinkwood), *Hedycarya arborea* (pigeonwood) and *Pseudowintera colorata* (pepperwood). Less common understorey species are *Aristotelia serrata* (wineberry), *Schefflera digitata* (pate), *Ascarina lucida* (hutu), *Carpodetus serratus* (marbleleaf), *Coprosma ciliata*, *Coprosma* sp.aff. *parviflora*, *Coprosma rotundifolia* and *Coprosma rhamnoides*. The tree fern *Dicksonia squarrosa* is common throughout the terrace forest and the tree fern *Cyathea smithii* occasionally occurs.

The ground layer consists of patchily distributed brypohytes and herbs such as *Nertera depressa*, *N.* sp. aff. *dichondraefolia*, *Astelia fragrans*, *Libertia pulchella*, *Astelia fragrans*, *Blechnum discolor*, and *Blechnum* sp 1. (kiokio). On the lower trunks of trees and on dead trees and branches, *Hymenophyllum species* and *Trichomanes reniforme* (kidney fern) commonly occur. Epiphytes and lianas occur in the crowns and on the trunks of the conifer and larger angiosperm species, and include occasional *Freycinetia banksii* (Kie Kie), *Asplenium* species, *Ripogonum scandens* (supplejack), and climbing ratas such as *Metrosideros diffusa* and *M. perforata* (Poole 1937).

The terrace forest of Saltwater Forest intergrades with pakihi wetlands and associated vegetation in Saltwater Ecological Area to the northwest (Norton, 1989; Norton & Leathwick 1990). Pakihi is a local term for a wetland vegetation type formed on low lying outwash surfaces below glacial moraines on recent alluvial surfaces. It consists of an open sedge/fern/restiad community grading into a more floristically diverse marginal forest (Norton 1989). To the southeast is conifer/angiosperm of Mt Hercules Scenic Reserve/Poerua State Forest. Kahikatea (*Dacrycarpus dacrydiodes*) forest occurs close to the Poerua river on the recent alluvial surfaces along the northern margin of the forest

(Norton & Leathwick 1990).

2.4 Geomorphology

Landforms in Saltwater Forest were largely formed by late Pleistocene glaciation as a result of both valley glaciers and piedmont ice sheets (Suggate 1965). The glaciers originated in the Southern Alps and during the Pleistocene extended beyond the alpine valleys out on to the piedmont plain, at times in some areas as far as the Tasman Sea (Almond, in press), with the most recent glacial advances leaving outwash gravels and tills belonging to the Moana Formation. The till and outwash gravels comprise Palaeozoic sedimentary, metamorphic, and igneous rocks (greywacke and argillite), of the Haast Schist and Tahua groups (granite) Almond (1986). Greywacke and schist rock groups are the most abundant, while argillite and granite are only a minor component of the drift (Almond 1986).

Much of Saltwater Forest consists of planar or gently undulating outwash terraces which decrease in elevation and slope towards the coast. The outwash surface has been dissected by late glacial and post glacial fluvial action resulting in an undulating landscape of terrace remnants, mounds, small rivers and streams. The small streams generally run from south to north. In the past, the landscape was shaped by a fluvial system which was more active than at present (Almond 1986). Currently the small streams are isolated in narrow, stable channels (incised up to 7m below the level of the dissected surface), that rarely, if ever, flood outside these channels.

A recent study by Almond (in press) has indicated three discrete periods of glacial advance that resulted in a complex system of differently aged terrace landforms. The oldest and most major advance (terrace 1) has been dated at greater than 22600 years B.P. due to the presence of Aoaokautere ash in the loess deposits in soils on this terrace. Terrace 1 exists as finger- like remnants of a previously extensive terrace that was dissected by meltwaters from the advance associated with terrace 2. The Aoaokautere ash is not present in the other two terraces, hence terrace 1 predates terraces 2 & 3. The following advance (terrace 2) occurred over terrace 1 in places, but in other areas incised through it due to its steeper gradient compared to the low lying

terrace 1. Terrace 1 and terrace 2 are aggradational surfaces, while terrace 3 comprises degradational terraces and relict channels formed when meltwater rivers incised into older till and outwash gravels. Terrace 3 is gently undulating in places which reflects the channels and sand bars of the meltwater river system. Almond (pers comm) suggests that terrace 2 is c. 18000 years old and terrace 3 is 14000-16000 years old. Terraces 1, 2 and 3 referred to in this study correspond to the terraces T4, T5 and T6 referred to by Almond (in press).

2.5 Soils

Saltwater forest has a water table which is high and close to the ground surface much of the year. There is very little water deficit in the forest soils, with run off occurring every month of the year. The high rainfall in combination with the high water table promotes a soil development environment where gleying and leaching are the dominant processes, resulting in the nutrient status of the soils being generally low (Mew & Palmer 1989).

Soils in Saltwater forest are related to the complex of landforms present (Almond 1986). Five general component landform classes have been recognised, levees, terraces, backswamps, mounds and remnant surfaces. Drainage is considered to be the key factor determining the characteristics of the soil (Sowden 1986, Mew & Palmer 1989). Across the terrace landforms, Almond (1986) recognised three different general soil classes ranging from poorly drained to very poorly drained. 'Saltwater' soils were poorly drained gley podzols formed in a veneer of stone free silt over alluvial gravels. The soils had a moderately thick O horizon over a grey, massive, firm silt loam that overlied humified alluvial gravels at 40-60cm depth. In some profiles, iron pans occurred within the gravels below the humus accumulation.

'Mall' soils include the mottled grey soils on terraces formed in gravelly alluvial fines. Characteristically a thin grey mottled horizon overlies a strongly ochreous mottled, stony gleyed subsoil. This in turn overlies a stony horizon with humus accumulation which is found within 50cm of the soil surface. The C horizon is olive or greyish brown alluvium in a coarse matrix. Mottling

indicates the presence of a fluctuating water table.

'Tunnel creek' soils are very poorly drained organic soils or peaty gleys which occur in low lying areas of the landscape with a high water table. The parent material is peat and alluvial silt. Characteristically, a black moderately decomposed organic horizon varying in thickness from 20cm to 80cm overlies a dark greyish brown silt loam muck ranging from 11 to 60cm thick. The muck is permanently saturated.

2.6 Climate

The West Coast has a consistently high rainfall, where long dry spells (15 days or more without rain) are rare. The combination of close proximity to the coast, and the Southern Alps acting as a barrier to prevailing westerly airflow, creates orographic rainfall which is often heavy and prolonged. During the year rainfall is relatively evenly distributed, but does show a weak seasonal pattern where spring rainfall is slightly higher than other seasons. Rainfall normals taken between the years 1951 to 1980 show HariHari has a mean annual rainfall of 3742mm (N.Z. Met. Ser 1983). Annual rainfall in Saltwater forest is likely to be similar to that in HariHari. Despite high rainfalls the sunshine averages are reasonably high and comparable to the east coast of the South Island; Hokitika on the west coast receives 1882 sunshine hours, and Christchurch on the east coast receives 1974 sunshine hours.

The maritime influence of the Tasman Sea produces a small range in mean annual temperature. The mean annual temperature at the study site has been calculated to be 11.7°C while the summer mean is 15.8°C and the winter mean 7.2°C (Norton 1985). Westland can be affected by very cold airstreams from the southwest/southeast, and very warm airflows from the north/northwest. Wind can blow from all directions, with most days of the year receiving only light winds. However at Hokitika for 12.2% of the time winds are strong and 0.5% of the time gale force winds exceed 74km/hr (Hessell 1982).

Chapter 3

Tree ageing problems

3.1 Introduction

Many of the results provided within this thesis rely on the interpretation of tree age data obtained from annual growth ring counts. Good age estimates were required to determine age-class frequency distributions to infer stand population dynamics. Therefore an assessment of the degree of error involved in estimating tree age is important.

Evidence of annual ring growth formation has been shown for many New Zealand species (Norton & Ogden 1987). However, several problems arise when using growth rings to study the age structure of New Zealand trees. These include non-annual growth ring production, ring wedging through lobate and eccentric growth, increment cores failing to reach the chronological centre and rings not accounted for due to the time taken to reach coring height (Norton et al. 1987). Previous studies have shown that these problems occur with *Dacrydium cupressinum* (Franklin 1969; Cornere 1992), the main species for which tree age was required in this present study.

In this chapter an estimate of the errors involved in estimating tree age at coring height for the more common conifers in the study area (*Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Lagarostrobos colensoi* and *Phyllocladus alpinus*) are evaluated.

3.2 Methods

Tree age estimates were obtained from cores taken from the longest axis of the trees at breast height (1.3m) to minimise errors from ring wedging and lobate growth. Cores were mounted on wooden blocks and air dried. Once the cores were dry the definition of annual growth rings was improved by

sanding with successively finer grades of sand paper. A binocular microscope was used to view the rings under reflected light. Ring width measurements were made using a Henson bench and the number of rings were recorded on the T.R.I.M.S. program (Madera Software 1986).

The age of trees that failed to reach the chronological centre due to increment core alignment, lobate or eccentric growth, short cores or rotten tree centres were estimated by assuming that the chronological centre was the trees geometric centre (see Norton et al. 1987). For cores which cut the inner growth rings the age of the missing portion was estimated using the geometric model of Duncan (1989).

3.2.1 Age to coring height

One of the problems inherent in ageing trees is the difficulty of obtaining a core at ground level unless destructive sampling is used. Cores taken at breast height result in an underestimate of tree age. Most evaluations of tree age based on increment cores in New Zealand have not estimated the age to reach coring height, although Stewart & Rose (1990) used a variety of methods to estimate this for *Nothofagus* species. Furthermore differences in time to reach coring height may occur between seedlings growing in the shade and those growing in open conditions (Ogden 1985a).

For the conifers the age to coring height was estimated from seedling age/height regressions for seedlings sampled from shaded and open conditions. For each category 30 seedlings were collected between 10cm and 200cm in height. Basal sections were taken from each seedling and mounted on a polystyrene block. The cross-section of each seedling was cleaned with a razor blade. Annual growth ring counts were made from the cross-sections viewed under a binocular microscope using reflected light.

3.2.2 Non circuit uniformity

The evaluation of tree age error estimates based on increment cores has been considered. However, this does not account for the variation that may occur in age estimates made along different radii at the same height for one tree. Norton (1986) found circuit uniformity (the pattern of growth rings along different radii at the same height) to be good in sub-alpine trees in New Zealand but suggests this may not be the case for trees located elsewhere. Non uniformity is likely to cause differences in the number of rings counted when cores taken from different radii miss the chronological centre.

For *Dacrydium cupressinum* and *Prumnopitys ferruginea* (species which possess variable ring patterns) four cores (at right angles to each other) were taken from each of four trees ranging from 15cm to 64cm dbh for *Dacrydium* and 13cm to 46cm for *Prumnopitys*. Tree age were then estimated for each core which missed the chronological centre but cut the inner arcs of rings as described by Duncan (1989). For each tree the percentage difference between the maximum and minimum age estimate was calculated. The age estimate of partial cores was not evaluated.

3.3 Results

3.3.1 Age to coring height

Age to coring height was determined for the conifer species from seedling/age height regressions (Table 3.1). Where possible this was estimated for seedlings growing in shaded and open light environments. However, seedlings of *Dacrydium* and *Phyllocladus* were only found in the shade. Seedlings of *Lagarostrobos* aged from a well lit site were found to be even aged (8 years) which suggests synchronous establishment, despite a difference in height of 190cm between the smallest and largest seedling aged. For seedlings growing in the shade *Phyllocladus* and *Dacrydium* took the longest to reach coring height. *Prumnopitys* seedlings growing in shaded and open conditions had the same age at coring height.

Table 3.1: Best fit regression equations for seedling age in years (Y) from height (X) and age to coring height (1.3m) for *Dacrydium cupressinum*, *Lagarostrobos colensoi*, *Prumnopitys ferruginea* and *Phyllocladus alpinus*. n = sample number. All regression models were significant at the p=0.001 level.

Species	Lighting	Regression equation	r^2	Age to coring height (1.3m)	n
Dacrydium cupressinum	Shade	Y=6.7+0.2X	0.73	36	30
Lagarostrobos colensoi	Open	.....	.....	8	30
Lagarostrobos colensoi	Shade	$\log_e$Y=2.2+0.7X	0.72	25	30
Prumnopitys ferruginea	Open	Y=8.8+14.3X	0.43	27	30
Prumnopitys ferruginea	Shade	Y=6.1+15.9X	0.81	27	30
Phyllocladus alpinus	Shade	√Y=2.8+0.02X	0.68	44	30

3.3.2 Non circuit uniformity

For both *Dacrydium* and *Prumnopitys*, practically identical mean levels of percentage age difference were found for estimating tree age from different radii from a range of diameters (Table 3.2). The percentage difference appeared unrelated to diameter and indicated an overall mean of c. 17% difference in estimates for both species, which for a 250 year old tree would result in an error of ±43 years.

Table 3.2: The minimum and maximum tree age differences for *Dacrydium cupressinum* and *Prumnopitys ferruginea* trees of different diameter. The minimum and maximum percentage differences are given calculated from the maximum possible difference (range) for a specific tree.

Diameter at breast height (cm)	Min estimate (years)	Max estimate (years)	Range (years)	% difference from min estimate	% difference from max estimate
Dacrydium cupressinum					
15	114	136	22	19	16
23	278	324	51	19	16
51	298	362	64	21	18
64	371	420	49	13	12
Prumnopitys ferruginea			Mean	18	15.5
13	173	224	54	31	24
22	255	317	62	24	20
37	310	326	16	5	5
46	366	421	55	15	13
			Mean	18.7	15.5

3.4 Discussion

Variation in age to coring height between species growing in well lit and shaded environments reflected different height growth responses to increased light levels. Such variation in height growth could result in an underestimate of age between eight and 44 years for trees aged at coring height, depending on the species and whether growing in shaded or well lit environments. The height growth response between shaded and well lit sites varied between two extremes. *Prumnopitys* showed no height growth response to increased light as was also found by Kell (1991), who found *Prumnopitys* to increase lateral branch growth only in response to raised light levels. By contrast *Lagarostrobos* showed the greatest height growth response to increased light. Seedlings of *Lagarostrobos* differed in age by 17 years between shaded and well lit sites. Differences in the response of *Dacrydium* and *Phyllocladus* to increased light is unknown as seedlings of both were only found in the shade.

Later in this study fifty year intervals are used to construct age-class frequency distributions, so by

not taking age to coring height into account could result in a tree being displaced down by one age-class, considering that the maximum age to coring height was 44 years. Most ages at coring height were within seventeen years of each other, such variation is likely to be within the fifty year age-class intervals used in this study, therefore tree age has not been adjusted in the subsequent analysis.

Differences in tree age estimate for *Dacrydium cupressinum* and *Prumnopitys ferruginea* suggest they have poor circuit uniformity. The age variation associated with this poor circuit uniformity was larger than that associated with age to coring height. However, the extent of non circuit uniformity in a stand for a particular species is unknown or whether this varies according to a trees growing environment. Similarly the percentage of samples that result in under estimates or over estimates in unknown. However, Cornere (1992) found an overall error of about 15% for estimating the true age due to missing rings for *Dacrydium cupressinum* of mean age 388 years in the same forest. This level of error was present when an increment core passed within 50mm of the chronological centre for the geometric model. A mean percentage error of 17% was found by Cornere (1992) for partial cores (cores which do not reach the chronological centre of the tree). The presence of non circuit uniformity highlights the importance of obtaining increment cores as close to the chronological centre of a tree as possible.

This study shows that errors associated with ageing trees at coring height can be large. These errors could result in erroneous interpretion of stand population dynamics, and will be more significant when comparing stands or species that have established under different light regimes, and when comparing species such as *Dacrydium* and *Prumnopitys* that have poor circuit uniformity. The errors involved suggest that 50 year age-classes are appropriate intervals to make relaistic comparisons of age-class frequency distributions between different stands, and between different species within stands.

Chapter 4

Variation in stand composition across the terrace forest

4.1 Introduction

In this chapter variation in stand composition across the three differently aged glacial terraces is assessed. Variation in species composition commonly reflects the distribution of species along environmental gradients. The terraces vary in age which can result in environmental variation related to stage of soil development, such as fertility, soil drainage and soil depth (Smith & Lee 1984; Sowden 1986). In Ianthe Forest, south Westland forest composition varies along a soil drainage gradient (Norton 1994). Similarly, landforms in Saltwater Forest are characterised by variation in soil types, and soil drainage (Almond 1986; Norton & Leathwick 1990). In addition, stage of forest development (stand structure), and differences in disturbance history can be equally important in determining forest composition (Stewart et al 1991). In this chapter assessment of the floristic variation is used to identify possible relationships to such environmental and disturbance factors.

4.2 Methods

Vegetation data were collected in unbounded plots (generally $400m^2$-$500m^2$) in the winters of 1991 and 1994 using a variation of the reconnaissance survey method of Allen (1992). Thirty plots were located on each terrace. Plots were located every 100m along randomly located transects. The first plot on each transect was located a random distance from the start of the transect. Distances were measured with hip-chain. On terrace 1 some of the plots fell in heavily logged areas. If this occurred the plot was located in the next intact area of forest at least 30m from the logged area. In addition, some of the plots fell in areas where occasional silver pine (*Lagarostrobos colensoi*) stems had been removed. Provided the structure was not markedly altered these points were sampled.

For each plot up to six physiognomic strata of variable height were recognised (ground, shrub,

understorey, sub canopy, canopy and emergent). For each stratum, all vascular species were recorded and their foliage cover assigned to a cover class (<1, 1-5, 6-10, 11-25, 26-50, 51-75, 76-100%). At each sampling point the angle of slope was recorded and drainage (a measure of the speed of run off and the degree of accumulation) assessed as either good, medium or poor.

The vegetation data were assessed using two multivariate techniques. Multivariate techniques have two basic roles in community ecology, to determine structure in the data and to produce relatively objective summaries (Greig-Smith 1983; Gauch 1986). A classification and an ordination technique were used. Ordination and classification techniques organise community data based exclusively on species abundance.

Classification was used to determine groupings of similar plots and samples to provide a framework for conceptualising different forest communities, even though in reality floristic variation is more likely to be a continuum. Ordination, was used to determine underlying compositional gradients. Both classification and ordination are effective at reducing "noise" (floristic variation associated with samples from the same community) and at summarising data "redundancy"(where many samples are much like other samples and many species resemble other species in their occurrences in samples), common problems associated with community data (Gauch 1986).

4.2.1 Classification

Before the data could be classified the species abundance data had to be transformed to an appropriate data matrix form. This was done using the programme RECINT (Hall 1992) which quantifies the ecological importance of the species observations. RECINT quantifies the ecological importance of the species observations within and between plots by constructing a table of species importance values. Importance values act as mathematical weights, whose relative sizes measure how similar or dissimilar one plot may be to another and hence what community classifications or ordination gradients are produced (Hall 1992).

An individual species importance value S_j is computed by summing the stratum weight (The default stratum weight of 1 was used) by the cover weight, i.e.

$$S_{ij}=\sum_{i=1}^{6}(t_i \times c_k)$$

where t_i,

i=1,...,6 are strata weights, one per stratum

c_k, k=1,...,n are the cover weights, one per class.

S_j is calculated for every species in a description.

Classification of the plots was undertaken based on their floristic composition using the RECINT output. Classification was performed using indicator species analysis (Hill et al 1975) as implemented in TWINSPAN (Hill 1979a). The basic assumption behind TWINSPAN is that groups of sites (plots) can be characterised by a group of differential species (Jongman et al 1987). Differential species are groups of species that appear to prevail on one side of a dichotomy. TWINSPAN is a polythetic divisive method (divides plots into groups based on all the species abundance information) that produces a hierarchical classification which shows relationships between different groups of species and plots. The classification of groups and plots is used to obtain a two way table that expresses their synecological relations. Data is first ordinated by reciprocal averaging. Then those species that characterise the reciprocal averaging axis extremes are emphasised in order to polarise the samples, the samples are then divided up into two groups by breaking the ordination axis near its middle. The sample division is refined by a reclassification using species with maximum values for indicating the poles of the ordination axis. The division process is then repeated on the two sample subsets to give four groups and so on until each group has no more than a chosen number. The relationships between the groups of species and groups of plots identified by the division process are displayed in a dendrogram.

Differences between samples are emphasised by the use of pseudospecies. This is a key point of TWINSPAN. The use of pseudospecies allows quantitative values of one particular species abundance to be partitioned into a series of pseudospecies which can then be used as differential species, and as indicators. Therefore, one species can for purposes of analysis be regarded as different species depending on its abundance and the cut levels set (Kent & Coker 1992). Another advantage of the use of pseudospecies is that it allows the correct transformation of a species response along a gradient. If a species abundance shows a unimodal response curve along a gradient, each pseudospecies also shows a unimodal response curve (Jongman et al 1987). In this present study the default pseuodospecies settings were used. Plots are initially classified by TWINSPAN. The subsequent species classification is based on fidelity, the degree to which particular species are confined to groups of plots (Jongman et al 1987).

Communities were subjectively determined from the dendrogram from knowledge of what realistically reflected forest variation. Identified communities were named following a hierarchical approach similar to Atkinson (1985) with the following modifications; no brackets around species indicate >10% cover, ( ) brackets indicate 5-10% cover and [ ] brackets indicate <5% cover.

4.2.2 Ordination

To interpret the vegetation pattern indirect ordination of the plots was performed using detrended correspondence analysis (DCA: Hill & Gauch 1980) as implemented in the program DECORANA (Hill 1979b). DCA derives ecologically meaningful ordering of sites (plots) and species, and it is one of the most powerful tools for representing pattern in communities composed of species that vary unimodally (Gausian species response curve) along underlying compositional gradients (Peet et al 1988). The result of ordination is the arrangement of species and samples along gradients such that similar species or samples are close by and dissimilar species or samples far apart (Gauch 1986).

DCA has advantages over other ordination techniques such as correspondence analysis (CA) in that it removes two problems. It removes the "arch" effect in which the second and subsequent axes

appear as a polynomial function of the first and thus obscuring the underlying gradient structure. Secondly it rescales the axes to provide readily interpretable units of length, removing distortion, particularly compression at the ends of the axes (Peet et al 1988). However, these two features have been criticised by Wartenberg et al (1988) for situations when analysis is applied to unimodal species distribution along a one-dimensional environmental gradient. They argue the arch effect is an important, inherent property where species response is a Gausian response. However, most data sets are collected from sites where a complex of factors can effect composition. When this occurs such problems do not arise (Peet et al 1988). Such an assumption is based on species varying along coenclines with simple unimodal species response curves. Analysis is further flawed when features of the environment result in a non-linear species response so that distortion of the underlying gradient occurs on account of rescaling and removal of the arch effect (Minchin 1987). In this present study I assume species display characteristic unimodal species response curves.

The impact of rare species on the ordination was down-weighted (the default setting). A rare species is any species whose occurrence is less than 20% that of the most common species. The results of the ordination were interpreted by comparing the four axes produced that summarise different amounts of floristic variation. An eigenvalue is associated with each axis. Generally the higher the eigenvalue the more significant the axis is at modelling the variation in the data (Hall 1992). However a significant drop in the eigenvalue from one axis to the next also suggests that the axes associated with the higher value, models much of the floristic variation even if the actual eigenvalue is relatively low. In addition, the four axes were plotted against each other to visually assess how interpretable the gradients were.

4.3 Results

4.3.1 Community classification

Five communities were identified from the indicator species analysis dendrogram (Figure 4.1). The mean percentage cover (cover classes are defined from the importance values used in the

Figure 4.1: Dendrogram from the ISA classification showing indicator species and the relationship between the five communities. Species codes are the first three letters of the generic and specific names for each species (see Table 1 for full names).

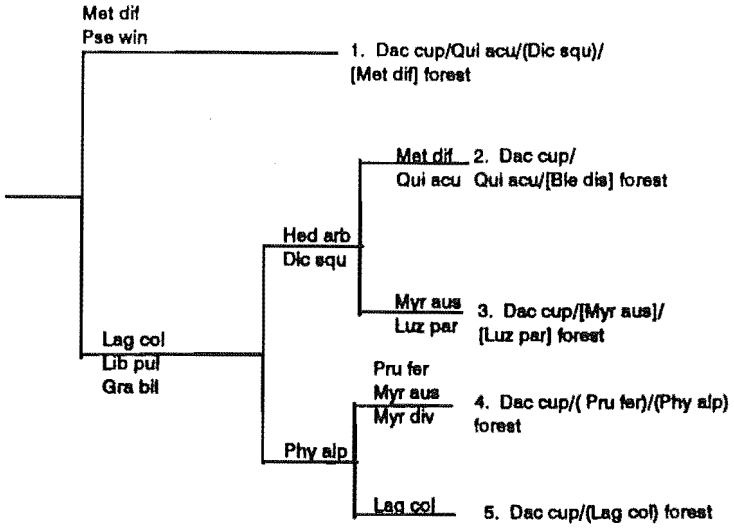


Figure 4.2: Scatter diagram of axis 1 and 2 of the plot ordination obtained from the DCA output with the distribution of plots on differently aged terraces superimposed.

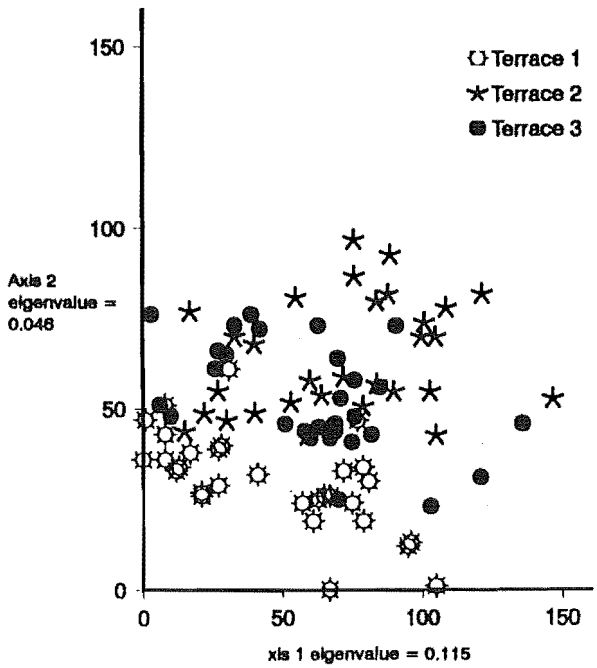


Table 4.1: Ordered species percent cover abundance matrix for those species present in >80% of any one community, .=species with <1%, += 1-5% cover in any one community.

	Community				
	1	2	3	4	5
Number of plots	20	10	14	27	19
Total # species	53	44	47	47	36
Species					
Coprosma ciliata			+		
Asplenium bulbiferum		+	+		+
Carex sp			+		
Hymenophyllum sp			+	+	+
Hymenophyllum scabrum					+
Lindsaea trichomanoides					
Lagarostrobos colensoi	+	3	2	2	8
Luzuriaga parviflora	+	+	.	+	+
Podocarpus hallii		+		+	
Grammitis billardieri	+	+	+	.	1
Coprosma lucida	+		+	+	+
Stlcherus cunninghamii	+	1	+	+	+
Uncinia sp	+	1	.	.	1
Libertia pulchella	+	1	+	.	+
Trichomanes reniforme	+	+	.	+	.
Phyllocladus alpinus	+	1	2	8	+
Coprosma colensoi	+	+	+	+	+
Elaeocarpus hookerianus	3	5	3	3	5
Griselinia littoralis	4	3	3	3	3
Coprosma foetidissima	2	3	3	3	3
Blechnum procerum	+	2	.	2	2
Blechnum sp 1. kiokio	+	+	+	+	+
Dacrydium cupressinum	10	10	10	11	12
Prumnopitys ferruginea	6	7	3	9	3
Weinmannia racemosa	16	17	15	14	13
Quintinia acutifolia	15	16	9	8	11
Pseudopanax colensoi	2	4	2	2	2
Pseudopanax crassifolius	3	3	3	3	3
Neomyrtus pedunculata	3	4	5	5	5
Nertera dichondraefolia	1	2	.	.	.
Astelia fragrans	+	+	+	+	+
Myrsine divaricata	+	+	+	+	+
Coprosma parviflora	+	+	+	+	+
Dicksonnia squarrosa	7	3	3	2	+
Blechnum discolor	2	2	+	+	+
Ripogonum scandens	+	+	+	+	+
Nertera depressa	1	.	+	+	+
Hedycarya arborea	+	2	2	+	
Asplenium flaccidum	+	+	+	+	
Cyathea smithii		+	+	+	
Phymatosorus diversifolius			+		
Ascarina lucida	+	+	+		
Myrsine australis	2	+	2	+	+
Hymenophyllum demissum	+	+	+	+	+
Dacrycarpus dacrydiodes	+	+		+	
Metrosideros diffusa	.	+	+	+	
Leptopteris superba	+	+	+	+	
Blechnum fluviatile	+	+	+	+	
Corybas rivularis	+		+	+	
Pseudowintera colorata	+	+	+	+	
Rubus cissoides	+				
Coprosma sp	+	+			
Aristotelia serrata	+			+	
Elaeocarpus dentatus	+				
Schefflera digitata	+				
Carpodetus serratus	+		+	+	
Melicytus ramiflorus	+				
Coprosma rotundifolia	+	+			
Coprosma rhamnoides	+			+	+
Microlaena avenacea	+			+	
Rubus australis	+				
Melicytus lanceolatus	+				

classification) summed over all strata of 62 species was used to summarise the vegetation differences between the communities (Table 4.1). For all communities the conifer *Dacrydium cupressinum* was the physiognomic dominant and generally dominated the canopy, while the understorey was dominated by the angiosperms *Weinmannia racemosa* and *Quintinia acutifolia*. However, cover of the conifers *Lagarostrobos colensoi*, *Prumnopitys ferruginea* and *Phyllocladus alpinus* varied considerably between communities. High abundance of *Prumnopitys* occurred with low abundance of *Lagarostrobos* and vice versa, which suggests a preference for different environmental conditions, or occurrence at different stages of stand development. Differences between the communities were also apparent in the cover of the angiosperm *Quintinia acutifolia*, the tree fern *Dicksonia squarrosa*, the small trees *Hedycarya arborea* and *Myrsine australis*, the ferns *Blechnum discolor* and *Grammitis billardierei*, and the climbing rata *Metrosideros diffusa*. The communities also differed in the number of species they contained, and in particular divaricating shrubs. For each terrace a particular community was dominant (Table 4.2). A brief description of the communities follows.

Table 4.2: The distribution of the communities across the terraces

	Frequency of communities			
Community	Terrace 1	Terrace 2	Terrace 3	Total
(1) *Dacrydium cupressinum/Quintinia acutifolia,Dicksonia squarrosa/[Metrosideros diffusa]* forest	1	15	4	20
(2) *Dacrydium cupressinum/ Quintinia acutifolia,/[Blechnum discolor]* forest	9	1	0	10
(3) *Dacrydium cupressinum /[Myrsine australis]/[Luzuragia parviflora]* forest	5	1	8	14
(4)*Dacrydium cupressinum,/(Prumnopitys ferruginea)/(Phyllocladus alpinus)* forest	3	8	16	27
(5) *Dacrydium cupressinum/ (Lagarostrobos colensoi)* forest	12	5	2	19
Total	30	30	30	90

1. *Dacrydium cupressinum/Quintinia acutifolia/Dicksonia squarrosa/*[*Metrosideros diffusa*] forest. (20 plots)

This community possessed 85% of all species recorded and was dominant on terrace 2. *Dacrydium cupressinum* occurred as scattered tall emergents and was occasionally present throughout the other strata. *Quintinia acutifolia* was abundant in the understorey and occasionally present in the subcanopy together with the conifer *Prumnopitys ferruginea*. The shrub layer contained a diverse range of small tree species, in particular pepperwood (*Pseudowintera colorata*) and divaricating shrubs such as *Myrsine divaricata*. The tree fern *Dicksonia squarrosa* occurred in abundance as conspicuous and tall specimens (2-3m). *Blechnum discolor* was common on the forest floor but the umbrella fern *Sticherus cunninghamii* was rare. Also common on the forest floor was the climbing rata *Metrosideros diffusa* and the herb *Nertera* sp aff. *dicondraefolia*.

2. *Dacrydium cupressinum/Quintinia acutifolia/* [*Blechnum discolor*] forest (10 plots).

This community occurred more frequently on terrace 1 than the other terraces and possessed 71% of all species recorded. The canopy was dominated by stands of *Dacrydium cupressinum* of similar height, however occasional *Lagarostrobos* and *Prumnopitys* were present in the subcanopy. Conspicuous tall *Quintinia* stems were also present in the subcanopy but less evident in the understorey where *Weinmannia racemosa* dominated. *Hedycarya arborea* was common as a small tree up to two metres but the small tree *Myrsine australis* was absent.

3. *Dacrydium cupressinum/* [*Myrsine australis*]/[*Luzuragia parviflora*] forest (14 plots).

This community was common on terrace 3, occasionally present on 1 and rare on terrace 2, and possessed 76% of all species recorded. The canopy was dominated by large and heavily branched stems of *Dacrydium*. The conifers *Prumnopitys* and *Lagarostrobos* were rare. The understorey and shrub layers were dominated by small stems of *Weinmannia*. The small trees *Myrsine australis* and *Hedycarya arborea* were common in the shrub layer, and the small tree *Pseudowintera colorata* was common in half of the plots. The kidney fern *Trichomanes reniforme* was common on fallen trees and rotting large branches.

4. *Dacrydium cupressinum*/(*Prumnopitys ferruginea*)/(*Phyllocladus alpinus*) forest, (27 plots)

This community was the most common and was dominant on terrace 3, and was frequent on terrace 2, but rare on terrace 1. The community possessed 76% of all species. It was characterised by scattered large heavily branched *Dacrydium* trees. The conifer *Prumnopitys ferruginea* was most common in this community, occurring as large subcanopy trees with occasional stems present in the understorey and shrub layers. Larger specimens of *Phyllocladus alpinus* commonly occurred in the shrub layer and also in the understorey in gaps with *Weinmannia*. *Quintinia acutifolia* was least common in this community. *Astelia fragrans* occurred as large individuals on the forest floor, mainly in the plots on terrace 3. *Libertia pulchella* and *Grammatis billardierei* were common on the forest floor.

5. *Dacrydium cupressinum*/(*Lagarostrobos colensoi*) forest, (19 plots)

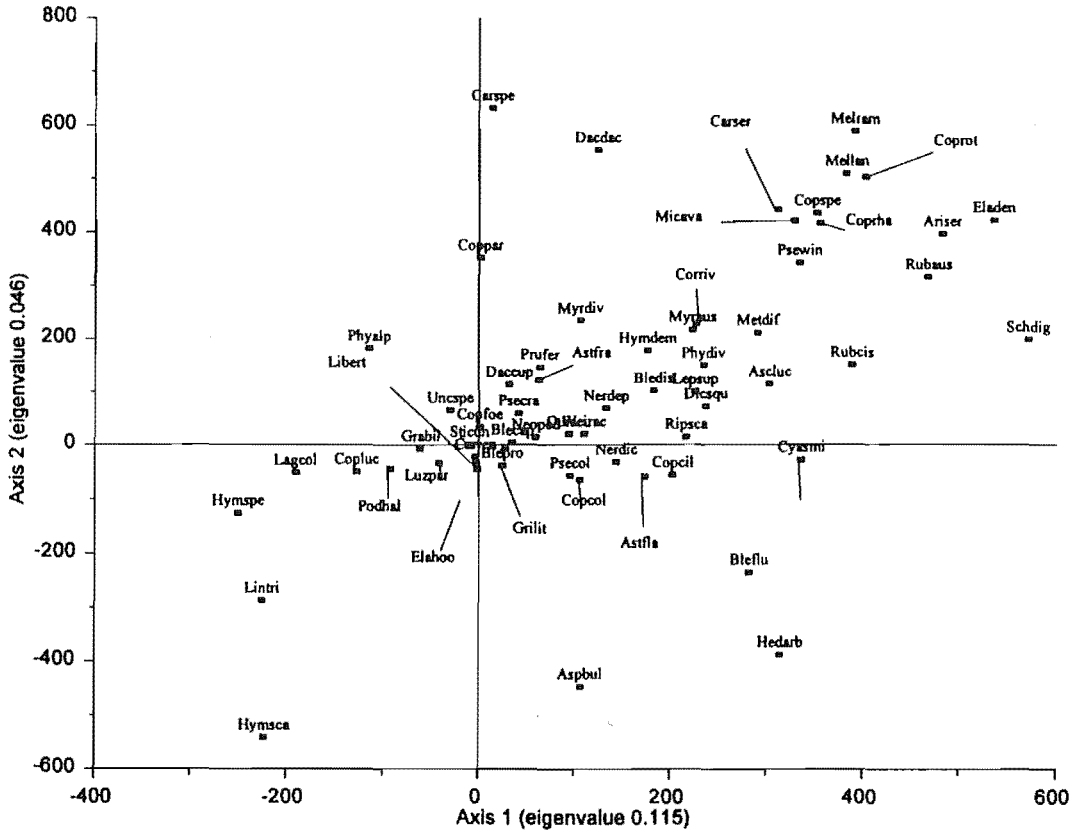
This community most frequently occurred on terrace 1 and possessed the least (58%) number of all species. Stands were the most uniform consisting of dense poles of *Dacrydium* and *Lagarostrobos* in the canopy and subcanopy. *Lagarostrobos* stems occasionally dominated. *Phyllocladus alpinus* was common in the understorey and or the shrub layer. Stems of *Weinmannia* and *Quintinia* were sparse in the understorey, with occasional tall stems of *Quintinia* in the subcanopy. The tree fern *Dicksonia* was rare and the less common ferns, divaricating shrubs and small tree species were generally absent. However the small tree *Coprosma lucida* occurred in half of the plots while it was less common in the other communities.

4.3.2 Plot and species ordination

Because of the difficulty in qualitatively determining drainage, no attempt was made to correlate drainage recorded to the species ordination gradient. Altitude was practically the same for all sites (32m) and all sites appeared to be relatively flat with zero aspect.

Axes one and two only were used to summarise the floristic gradients. Other combinations of axes could not be interpreted, and the relatively large drop in eigenvalue from axes 1 to axes two suggests

Figure 4.3: Axis 1 and 2 of the DCA species ordination. Full species names are given in table 1



axes one models much of the floristic variation present. The relatively wide spread of plots in the ordination diagram (Figure 4.2) suggests that the distribution was related to more than one environmental gradient, while the partial segregation of the plots suggests that environmental variation between terraces was significant. Plots on terrace 1 were associated with low scores on axes one and two of the ordination diagram, overlapping least with plots from terrace 2. This suggests that terrace 1 plots were most floristically distinct from terrace 2 plots. Some plots on terrace 2 overlapped considerably with those from terrace 3 reflecting floristic similarities, while others on terrace 2 were associated with higher scores on axes 1 or 2 reflecting floristic differences. Although there was a general trend of increasing floristic difference from plots on terrace 1 to those on terrace 2, the relatively short length of the axes at less than 1.5 standard deviations reflects that even plots at opposite ends of the axes have a number of species in common.

The species ordination suggests a distinct compositional gradient from low scores on axes 1 and 2 (species more commonly associated with communities on terrace 1, e.g., community 5) to high scores on axes 1 and 2 (species more commonly associated with terrace 2, e.g., community 2) (Figure 4.3).

4.4 Discussion

The distribution of species along environmental gradients has been documented in south Westland between different landform types (Norton & Leathwick 1990; Duncan et al. 1990; Norton 1994). However in this present study a floristic gradient was associated with one landform type (terraces) as reflected by the different community compositions and plot and species ordination.

Previous studies considered heterogeneity in forest composition across the terrace forest primarily related to stand age (Six Dijkstra et al. 1985). However here floristic composition reflected differences in terrace age that could reflect changes in edaphic conditions, e.g., soil drainage and fertility. On stable landforms such as the glacial terraces in Saltwater Forest soil development has proceeded unaffected by major disturbances for long periods (cf. Basher 1986; Stewart & Harrison

1987). Under high rainfall areas in Westland a trend of deteriorating drainage and increasing soil depth occurs on lowland forest sequences with increasing landform age (Smith & Lee 1984; Sowden 1986), although Sowden (1986) notes that most of the differences occur between 0-300 years in his study area. Floristic variation between the terraces could reflect such differences in soil development, and in particular soil drainage. In which case the uniform *Dacrydium cupressinum, Lagarostrobos colensoi* forest type dominant on terrace 1(the oldest terrace) may reflect a community most suited to impoverished soil conditions associated with an advanced stage of soil development, while the *Dacrydium cupressinum, Prumnopitys ferruginea, Phyllocladus alpinus* forest type dominant on terrace 3 (the youngest terrace) may reflect less well developed younger soils. Similar changes in forest composition have been described for Saltwater Ecological Area (Norton & Leathwick 1990) and reflected the difference between poorly drained sites around the edges of mires and moderately drained gently sloping and flat sites.

The compositional gradient of the species ordination could be interpreted as reflecting a soil drainage/fertility gradient. Species associated with low scores on axes 1 may reflect the most poorly drained sites, e.g., *Podocarpus hallii, Phyllocladus alpinus* and *Lagarostrobos colensoi* have been associated with poorly drained older surfaces, while *Schefflera digitata, Carpodetus serratus*, and *Dacrycarpus dacrydiodes*, which were associated with higher scores on axes 1 and 2, occur on more fertile, less poorly drained sites (Norton & Leathwick 1990).

Norton (1994) found the pteridophyte distribution in the nearby Ianthe Forest was primarily affected by differences in soil drainage associated with different topographic positions. *Blechnum procerum* favoured poorly drained sites while *Blechnum discolor* favoured better drained sites. If the floristic gradient in this present study primarily reflected differences in soil drainage, these species may be expected to occur at opposite ends of the gradient. This was not so as they were relatively close together, occurring at just under 0.2 standard deviations apart over a total gradient length of c. 0.9 along axis 1. It may be that stand structure was also a significant factor affecting their distribution so that changes normally associated with edaphic conditions were less distinct.

The distribution of *Lagarostrobos colensoi* has been related to poorly drained sites, stage of forest development and disturbance pattern. Six Dijkstra et al. (1985) suggested that *Lagarostrobos* was generally out competed by *Dacrydium* trees as a stand matured, while Ogden & Stewart (1995) suggest *Lagarostrobos* primarily persists on sites that are both wet and have been catastrophically disturbed. For this present study the position of *Lagarostrobos* on the ordination axes, associated with low scores on axes 1 and 2 presumably reflects a combination of these factors, so that species associated with higher scores on axes 1 and 2 reflect their occurrence in stands at a later stage of forest development, occurring on less poorly drained soils.

Floristic variation (species richness) was also associated with differences in stand structure between the communities. The most uniform stands had the lowest number of species (community 5 dominant on terrace 2) while the highest number of species occurred where stand structure was more varied (community 1 dominant on terrace 2). A more varied stand structure would create a heterogeneous environment allowing opportunities for species with greater niche differentiation than in a uniform stand (Whittaker 1975). Although such niche-differentiation mechanisms are important, differences in composition between the communities could also reflect differences in disturbance history as reflected by changes in stand structure (Armesto & Pickett 1985, Stewart et al 1991).

Although the interpretation of relationships has been hindered by the limited environmental data it appears that for the terraces in Saltwater Forest floristic variation is related to surface age and stand structure. However what proportion of forest variation these factors contribute to and what mechanisms are involved are unclear. The following sections focus on these aspects.

Chapter 5

Stand structure variation within terraces

5.1 Introduction

Having established in chapter 4 that floristic and stand structural variation across the terraces is associated with terrace age, this section examines in more detail the stand characteristics (size-class frequency distributions, stem density, basal area) associated with the different terraces . These are then related to the forest communities identified in chapter 4.

5.2 Methods

Variation in forest structure on each terrace was assessed from the size class frequency distributions of the main conifer species *Dacrydium cupressinum*, *Lagarostrobos colensoi* and *Prumnopitys ferruginea*. The location of the sample plots (40m×40m) was determined from differences in canopy texture present in monochrome aerial photos (scale 1:25000). These were used to identify and locate different stand types in the field. Differences apparent in the aerial photos were assumed to reflect differences in canopy species composition and stem diameter distributions. For each plot population size structures were determined from the dbh of all live conifers (≥5cm dbh at 1.3m height). Stem density and basal area were calculated for the conifers in each plot. Nine plots were located on terrace 1, four on terrace 2 and two on terrace 3 reflecting the number of differe0nt stand types identified for each terrace from the aerial photos.

The population dynamics of each plot was interpreted from the shape of the size class frequency distributions and from a sample of tree ages. The distribution of stems in different size classes within a given stand commonly reflects the mode of regeneration of the constituent tree species (Veblen & Stewart 1980; Veblen 1992). Three general regeneration patterns are recognised, catastrophic, gap-

phase and continuous (Veblen 1992). Tree ages were determined from a selection of the plots to reflect the range of stand structures present on each surface. One tree was aged from each of up to six 10cm size classes beginning at 5-14cm dbh taken from *Dacrydium* and *Lagarostrobos* stems only (for details of tree ageing see chapter 3).

5.3 Results

5.3.1 Stand structure of the 40m×40m plots

The size-class frequency distributions and the sample of tree ages indicated that stand and age-structure varied both between and within terraces (Figure 5.1). The fifteen stands sampled across the three terraces ranged from *Dacrydium cupressinum* dominated stands with stems up to 94cm dbh (Stands 1.1, 1.2, 1.3, 1.4, 1.6, 2.1, 2.2, & 3.1) to those dominated by *Lagarostrobos colensoi* and smaller diameter *Dacrydium* (1.5, 1.7, 1.8, & 3.2).

The shape of the size-class frequency distributions of the stands varied from distinct unimodal distributions suggestive of even-aged populations (e.g. stand 1.4), to more sporadic distributions suggestive of all-aged populations (e.g. stand 2.1), to reverse 'j' shaped distributions (e.g. stand 1.9). The latter size-class frequency distribution could indicate a continuously regenerating population or an early developmental stage of an even-aged population.

Dacrydium dominated stands generally possessed broad unimodal size-class frequency distributions while the distribution of *Dacrydium* in stands 1.6 and 3.1 was suggestive of older groups of trees. The exception were the four stands on terrace 2. Here *Dacrydium* was more sporadically distributed between size-classes. *Prumnopitys ferruginea* was most abundant in stand 1.3 where there was no *Lagarostrobos colensoi*. *Lagarostrobos* dominated stands possessed up to thirteen times more *Lagarostrobos* stems than *Dacrydium* stems and in general had a high stem density in comparison to *Dacrydium* dominated stands (Table 5.1). *Lagarostrobos* size-class frequency distributions were generally unimodal, suggestive of even-aged populations.

Table 5.1: Density (stems ha^{-1}) and basal area (m^2ha^{-1}) for the stands sampled across terrace 1,2 & 3. NP= species not present.

		Dacrydium cupressinum		*Lagarostrobos colensoi*		*Prumnopitys ferruginea*	
	Stand	Stems ha^{-1}	Basal area ha^{-1}	Stems ha^{-1}	Basal area ha^{-1}	Stems ha^{-1}	Basal area ha^{-1}
Terrace 1	1.1	294	57.6	NP	NP	44	3.8
	1.2	375	68.9	NP	NP	38	3.5
	1.3	400	60.7	NP	NP	113	6.7
	1.4	531	66.9	NP	NP	NP	NP
	1.5	456	29.7	363	15.3	6	0.02
	1.6	88	29.3	NP	NP	44	1.4
	1.7	64	13.5	863	39.1	NP	NP
	1.8	325	15.9	1163	48.4	44	1.4
	1.9	438	23.4	169	5.9	75	1.9
Terrace 2	2.1	119	23.6	0	0	100	3.8
	2.2	169	34.5	60	1.1	19	0.8
	2.3	319	38.3	294	4.2	31	0.6
	2.4	388	39.2	50	1.2	25	1.6
Terrace 3	3.1	23	45.3	0	0	2	0.1
	3.2	350	102.4	294	104.2	0	0

Although relatively few stands were sampled across the terraces, areas of the different stands present in the aerial photos together with knowledge of the terrace forest suggested that one stand type was dominant across each terrace. Dense uniform *Lagarostrobos/Dacrydium* stands dominated terrace 1 (stands 1.5, 1.7 and 1.8) which may reflect that community 5 is dominant on terrace 1, while stands across terrace 2 were less uniform in structure as for stands 2.1 and 2.2 reflecting community 1. Terrace 3 stands appeared least dense, dominated by larger *Dacrydium* as for stand type 3.2. More compelling evidence of the association of stand types with terrace age would be to determine the exact areas in the aerial photos that correspond to the different stand types. However, because of logging and the difficulty of locating exact boundaries of the differently aged terraces this was not done.

Figure 5.1: Size-class frequency distributions for stands 1.1-1.6, terrace 1. Size classes are 10cm intervals beginning at 5-14cm dbh.

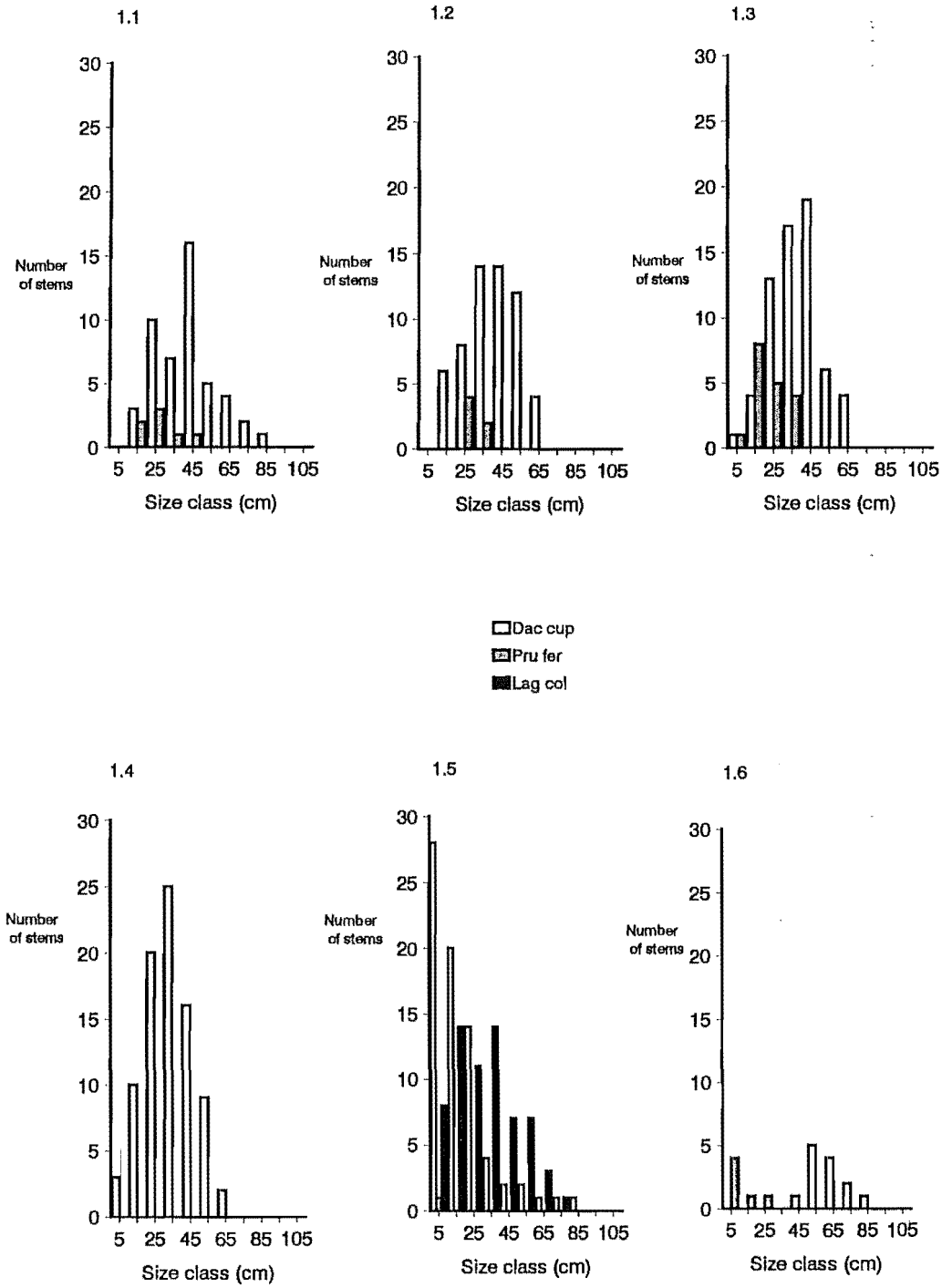


Figure 5.1 (continued): Size-class frequency distributions for stands 1.6-1.9, terrace 1 and 2.1-2.3 terrace 2. Size classes are 10cm intervals beginning at 5-14cm dbh.

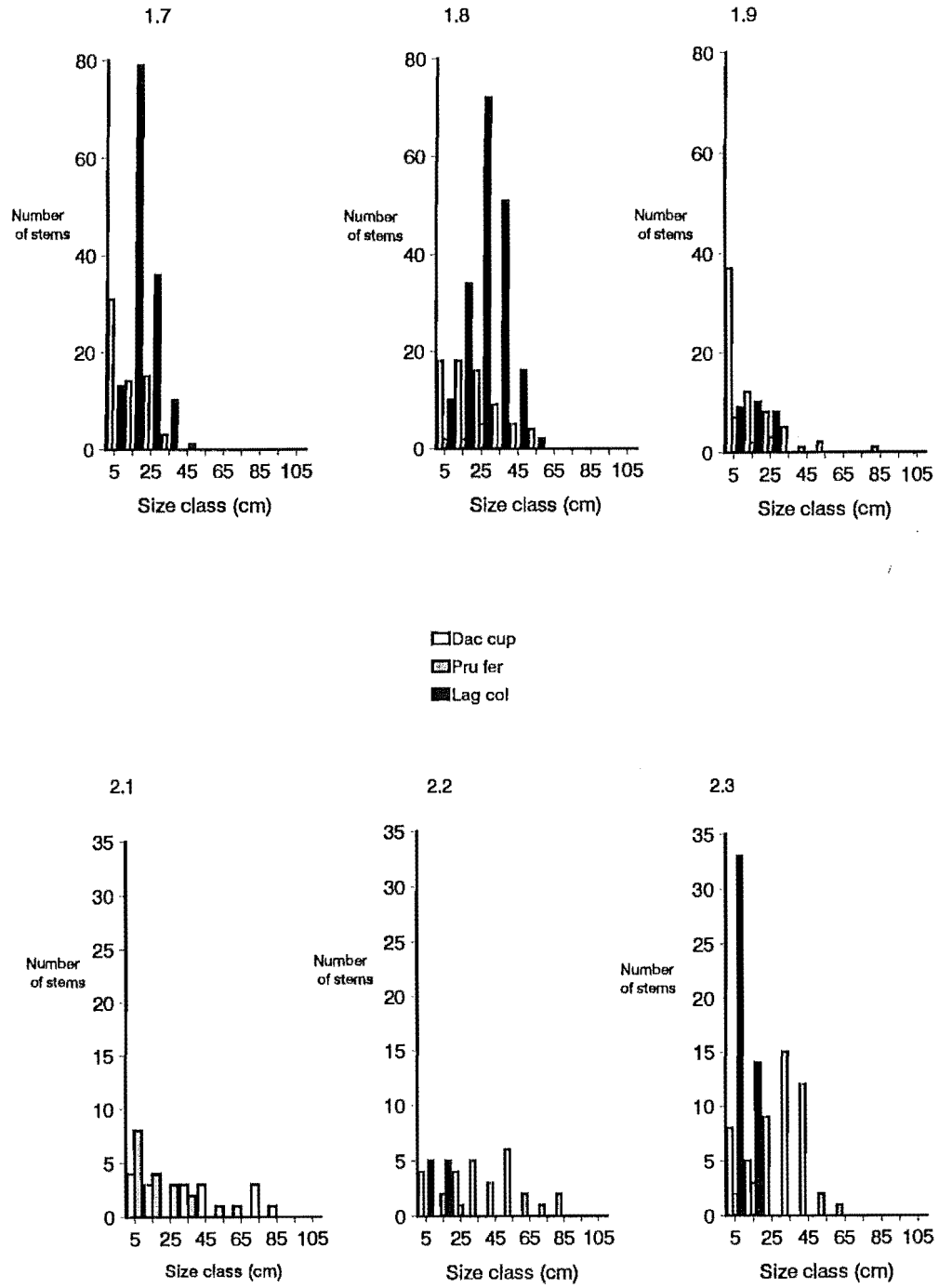


Figure 5.1 (continued): Size-class frequency distributions for stands 2.4, terrace 2 and 3.1 and 3.2 terrace 3. Size classes are 10cm intervals beginning at 5-14cm dbh.

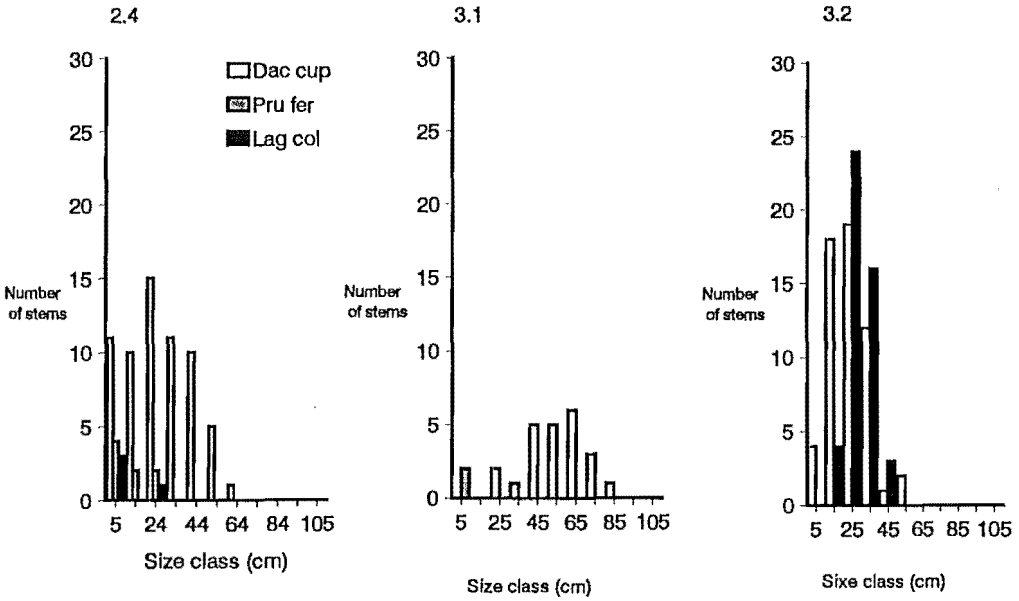
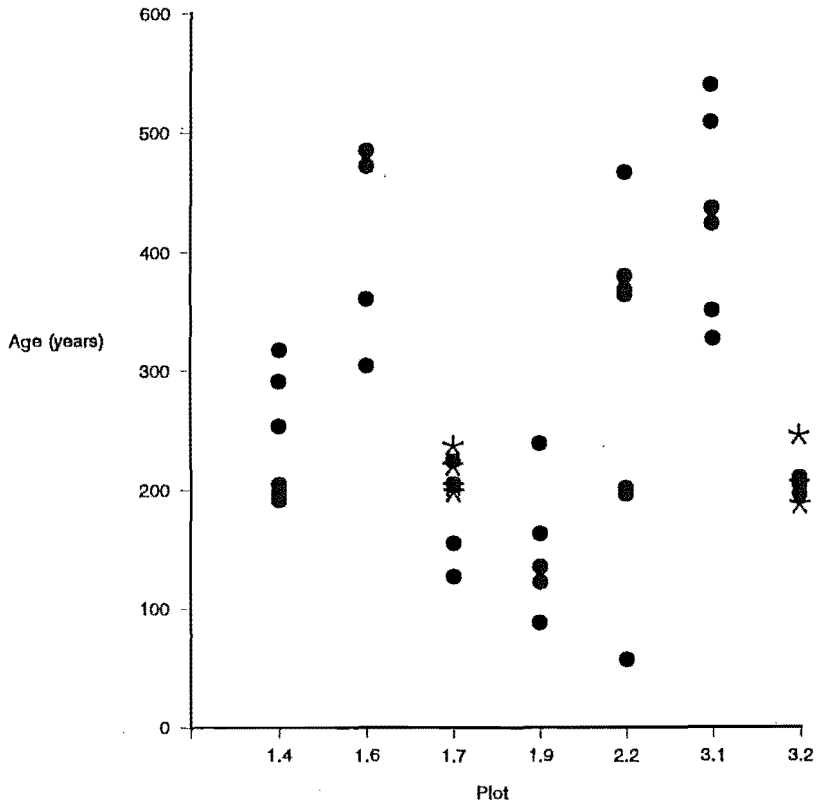


Figure 5.2: Age distributions for *Dacrydium cupressinum* (dots) and *Lagarostrobos colensoi* (asterix) in stands 1.4, 1.6, 1.7, 1.9, 2.2, 3.1 and 3.2.



5.3.2 Tree ages for the 40m×40m plots

Although the sample size is limited, the sample of tree ages for *Dacrydium* from stands 1.4, 1.6, 1.7, 1.9, 2.2, 3.1, & 3.2 (one per size-class present) suggests that most stands had discontinuous age ranges with the exception of stand 2.2 on terrace 2 which was more sporadically aged up to 460 years (Figure 5.2). The dense *Dacrydium* dominated and *Lagarostrobos* dominated stands (stands 1.4, 1.7, 1.9, & 3.2) were younger and had narrower age ranges than the stands 1.6 & 3.1 dominated by large diameter *Dacrydium*.

5.4 Discussion

Variation in stand structural types across the terraces could reflect separate stages of one stand development sequence. Six Dijkstra et al (1985) selected five stands to illustrate the regeneration cycle of terrace forest. The stands identified in this present study could be interpreted as reflecting floristic and structural changes associated with the Six Dijkstra et al (1985) model.

The high stem density *Lagarostrobos/Dacrydium* dominated stands 1.5, 1.7, 1.8 and 3.2 reflects the early competition growth phase of the Six Dijkstra model, while dense *Dacrydium* dominated stands 1.1, 1.2, 1.3, and 1.4 reflect the early competition growth phase where stems of *Lagarostrobos* have been out competed by faster growing *Dacrydium*. Later mature stages of the model, the early and late homeostatic growth phases are most similar to stands 1.6, 2.1, 2.2 and 3.1 where the stem density of *Dacrydium* is much lower and large diameter *Dacrydium* trees dominate in association with occasional *Prumnopitys* stems.

An alternative explanation is that variation in stand structure reflects different disturbance histories on differently aged terraces, where stand composition and size-class frequency distributions reflect a regeneration response to different spatial and temporal patterns of disturbance. Large scale disturbance may be associated with unimodal size-class frequency distributions reflecting even-aged regeneration (e.g. stand 1.4), while rarely disturbed stands may be associated with reverse "j" shaped

distributions reflecting continuous regeneration (e.g. stand 1.9). However, such size class frequency distributions are inconclusive as they can be misleading unless an age diameter relationship is shown (Stewart 1986). For this reason they are only used here as indicators to direct further inquiry.

It is unclear whether the described variation in stand structure reflects stage of forest development, differences in disturbance history or both. Stand structures were highly variable within and between terraces. The occurrence of stands at different stages of development is a good explanation of this, however an alternative explanation is that such variation reflects different patterns of stand development associated with variation in the effects of disturbance. Presuming windstorms are a dominant disturbance type, variation in disturbance effects must relate to differences in stand stability. Patterns of stand development and disturbance histories are investigated in more detail in the following chapter.

Chapter 6

Variation between the dominant stands on each terrace

6.1 Introduction

It has been established that stand composition and structure vary between the terraces, with one community type and stand structure dominant across each terrace. This section examines the dominant stand type on each terrace in more detail to determine whether this forest variation simply reflects stand age, or whether it is linked to environmental variation and differences in disturbance history associated with terrace age.

6.2 Methods

6.2.1 Plot Locations

For detailed analysis of the dominant stand type present on each of the three terraces one 0.4ha plot (100m×40m) divided into 5m×5m contiguous quadrats was located in the dominant stand structure on each terrace, away from past logging effects. Based on the 40m×40m plot descriptions (Chapter 5), for terrace 1 the most prevalent stand type had a high stem density of relatively small diameter *Dacrydium* and *Lagarostrobos* stems, while the dominant stand type on terrace 2 was a lower density stand with fewer *Lagarostrobos* but more *Prumnopitys* stems, with *Dacrydium* stems present in most size classes up to 95cm dbh. The dominant stand type on terrace 3 had the lowest stem density and was dominated by large *Dacrydium* and *Prumnopitys,* with relatively few small stems present (Chapter 5). The location of the three stands S1, S2 and S3 coincided with the location of one of the vegetation description plots that characterised the dominant community type on each terrace.

6.2.2 Stand Descriptions

Stand descriptions were initially made by determining the vertical structure , basal area and stem

density of the three stands (≥ 5cm dbh at 1.3m height). All live, and dead trees that could be identified were counted in each contiguous quadrat. Each tree was assigned to one of the relative height classes (1=shrub layer, 2=understorey, 3=subcanopy, 4=lower canopy, 5=upper canopy and 6=emergent).

6.2.3 Population structure of the three main stands (S1, S2 & S3)

Population size-structures when used in conjunction with age-structures can be used to assess the population dynamics of forest stands. However this is dependant upon establishing a relationship between tree size (diameter) and age (Stewart 1986). The interpretation of size structures is problematic because of variability in growth rates caused by differences in stand structure and environment (Parker & Peet 1984).

Population size structures were determined from the dbh of all live trees (≥ 5cm dbh at 1.3m height) for the main species in each contiguous quadrat. Counts of all conifer saplings (≥ 1.3m tall & < 5cm dbh), estimates of angiosperm saplings and estimates of angiosperm and conifer seedling numbers (0.1m-1.3m height) were made. Different sampling regimes were used for different species because of vast differences in abundance. For *Dacrydium*, *Lagarostrobos* and *Prumnopitys* numbers of seedlings and saplings were much lower compared to *Weinmannia* and *Quintinia* for which a less intensive sampling scheme was used. *Phyllocladus* seedling and sapling numbers appeared highly variable and so were sampled as for *Weinmannia* and *Quintinia*. For *Dacrydium*, *Lagarostrobos*, and *Prumnopitys*, saplings were counted in every 5×5m quadrat while seedling populations were estimated from counts in a systematic sample of every other 5×5m quadrat.

For *Phyllocladus alpinus*, *Weinmannia racemosa* and *Quintinia acutifolia* seedling counts were made from a systematic sample of three transects situated parallel to the longest side of the plot, and located at equal distances across the plot. Seedling counts were made in 0.9m×0.9m quadrats placed every 10m along each transect at the intersection points of the 5m×5m grid. Thirty points

were sampled in total for each plot. The same sampling locations were used for the sapling counts. All saplings were counted within the 5m × 5m quadrats adjacent to the seedling sampling quadrats.

Population age structures were determined from annual growth-ring counts (Chapter 3). A core was taken at breast height (1.3m) from each tree except for *Phyllocladus alpinus* in stand S2 where every fourth tree was cored because of the high stem density. Annual ring formation in *Weinmannia racemosa* and *Quintinia acutifolia* was found to be indistinct and could not be measured. However Norton & Ogden (1987) gives an example of good ring formation in *Quintinia acutifolia* and Stewart (1986) aged *Weinmannia racemosa* successfully from Fiordland.

For increment cores that failed to reach the chronological centre, unmeasurable cores, and for the *Phyllocladus* not aged, ages were fitted from regression models. The assumption was made that diameter and age were related so that ages could be estimated. An age diameter regression model was computed for the conifers in each of the three main plots using SAS (Statistical Analysis System). Regression models were accepted based on the distribution of the residuals. Normally distributed residuals indicated an unbiased regression model.

In addition to Stand S1 an adjacent stand was sampled (stand S1r) to determine the population characteristics of an earlier stage of stand development not evident in the main stand. Here a 10m×10m plot was located within a dense stand of *Dacrydium* saplings and young trees. All seedlings and saplings of the conifers were counted and their dbh measured for stems ≥5cm dbh at 1.3m height. *Weinmannia* and *Quintinia* were not counted as they were uncommon. Ages were determined from increment cores taken from ten small trees and from six cross sections taken from saplings at 1.3m height.

6.2.4 Spatial patterns

The spatial pattern of plants is an important characteristic of ecological communities and is defined

by ecologists as a non-random spatial abundance of organisms (Greig-Smith 1979). Early work by ecologists concerned with pattern focused on testing the hypothesis that a species exhibits a complete spatially random pattern, however few organisms exhibit complete spatial randomness (csr) at all scales so attention turned to the description of non-csr pattern (Ver Hoef *et al.* 1993).

Spatial pattern is expressed as a departure from a random distribution, displayed as a clumped or regular arrangements of individuals. An important feature of spatial pattern is the scale of pattern at which differences in abundance occur, the size of patches for instance and also intensity, which is the extent to which abundance differs over an area (Pielou 1977).

The biological significance of pattern may be attributed to morphological, environmental and sociological causes (Kershaw 1964, Greig-Smith 1983). Different scales and intensities of pattern occur on a continuum (Greig-Smith 1979), as a result of one or a few factors having a disproportionate effect on the performance or survival of a species. The distribution of that species will tend to be determined by that particular factor or factors (Greig-Smith 1983). At large scales aggregated patterns are attributed to environmental heterogeneity while at smaller scales environmental variation will be less prominent and species interactions become increasingly prominent (Diggle 1983).

This study focuses on the medium scale of pattern which can reflect site heterogeneity and regeneration in different sized disturbance openings, and the small scale pattern reflecting species interactions and establishment site preferences. Common approaches to sampling pattern have involved frequency counts for natural sampling units, a quadrat approach for artificial sampling units and plotless sampling techniques involving measurement of distance to nearest neighbour or distance to point measurements. Results from the quadrat approach are reliant upon the size, shape and orientation of the quadrats, except for random distributions (Pielou 1974). Interpretation of the results are based on the variance to mean ratio. Plotless sampling techniques avoid the problems

inherent in the quadrat approach but are limited to the detection of pattern up to the distance of the nearest neighbour (Greig Smith 1983, Pielou 1974).

The simplistic approach of random, clumped and uniform patterns has been improved by the use of a multidimensional approach obtained by identifying a continuum of different scales of pattern in one plane. This approach has been used here. The method used follows that described by Duncan (1991) and compares the distribution of all interplant distances with that expected from randomly dispersed trees. Pattern can be detected at any scale up to half the length of the shortest side of the plot.

Patterns of single species were analysed using the function L(t), a transformation of the function K(t) (Ripley 1976, 1977), suggested by Besag (1977).

$$L(t)=\sqrt{\frac{K(t)}{\pi}}-t$$

The function K(t) uses all interplant distances to provide a measure of spatial pattern at various distances (t). Under the model of complete spatial randomness the function L(t)=0. Values of L(t) > 0 indicate clumping at the distance t. Values of L(t) < 0 indicate a uniform distribution. Monte Carlo simulation is used to test the statistical significance of deviations of L(t) from 0 under the hypothesis of complete spatial randomness. Ninety-five percent confidence envelopes were generated from high and low values of the function L(t) obtained from 19 simulations of the random process.

6.2.5 Species interactions

The spatial pattern of a pair of species is of interest as it can indicate species interactions during stand development. Species interactions can reflect a variety of processes from competition for limited resources to allelopathy. A species may be positively or negatively associated with respect

to another species. Negative association is present when the presence of one of the species makes that of the other less likely (Pielou 1974). Positive association occurs when the presence of one of the species in any space or sampling point makes it more likely that the other will be found.

Negative association may indicate competition for limited resources or equally heterogeneity in the habitat when the habitat is made up of patches of ground suitable for one or other of the species. (Greig-Smith 1983). Positive association may indicate that a habitat varies smoothly where conditions optimum for one species are adjacent to but do not overlap those optimum for the other. Alternatively it could show that individuals of both the species, although they are competing fiercely for identical resources can grow larger when needed resources are relatively abundant (Greig-Smith 1983 & Pielou 1974).

The spatial pattern of pairs of species point locations was determined by use of the bivariate function L12(t) (Lotwick & Silverman 1982).

$$L_{12}(t)=\sqrt{\frac{K_{12}(t)}{\pi}}-t$$

Under the model of spatial independence L12(t)=0. Values of L12(t) >0 indicate positive association (attraction) between a pair of species point locations at that distance t. Values of L12(t)<0 indicate a negative association (repulsion). Monte Carlo simulation was used to test the statistical significance of deviations of L(t) from 0 under the null hypothesis of spatially independent components (i.e. no spatial association). Ninety-five percent confidence envelopes were generated from high and low values of the function L12(t) obtained from 19 toroidal shifts of one species with respect to the other (see Lotwick & Silverman 1982: Upton & Fingleton 1985, pages 253-254)

The univariate and bivariate statistics were computed using the X and Y coordinates of all stems (≥

5cm dbh & ≥ 1.3m height) measured to the nearest 10cm.

6.2.6 Seedling and sapling establishment patterns

Forest variation partly occurs along environmental gradients which are commonly associated with changes in soil moisture and fertility (Whittaker 1975). However, environmental variation can also reflect the occurrence of suitable establishment sites where species preferentially establish. Both microtopography and establishment substrate are important for seedling establishment and can be critical in determining stand structure and future canopy composition (Duncan 1993).

Here the establishment sites of the main tree species were recorded as log, mound (mounds were produced from the uprooting of trees and from stumps in an advanced state of decay) and forest floor, for each seedling counted (see population estimates). Establishment site was also recorded for each sapling counted for the angiosperms *Weinmannia racemosa* and *Quintinia acutifolia* and the conifer *Phyllocladus alpinus*. Since saplings of *Dacrydium*, *Lagarostrobos* and *Prumnopitys* were generally uncommon their establishment site was not recorded. The percentage of the different substrates present within the stand was compared to the percentage of seedlings present on the different establishment sites. The percentage of different establishment sites present was estimated by splitting the plot into four equal segments and locating 25 random points within each at intersections of the 5 × 5m grid.

Establishment patterns may also reflect the patchy distribution of different light levels throughout the stand as a consequence of different sized disturbance openings. Different species respond differently to light depending on their degree of shade tolerance. The creation of gaps in the forest canopy results in changes in the quality and quantity of light in the forest understorey micro-environment, presenting a complex, changing, and heterogeneous light environment (Endler 1993). Differences in canopy structure will affect the distribution of light within a stand (McDonald & Norton 1992). Therefore stands which differ in their canopy structure could have contrasting patterns of

seedling establishment. To assess the importance of the canopy light environments for the establishment of *Dacrydium*, *Lagarostrobos*, and *Prumnopitys* seedlings the percentage canopy cover was recorded in one of six canopy cover classes (1=<1, 2=1-5, 3=6-25, 4=26-50, 5=51-75, 6=76-100%) for each 5m×5m quadrat in which seedlings were counted. The canopy cover classes were subjectively assessed from a visual estimate at eye level of the sky blocked out by the canopy trees.

6.2.7 Spatial distribution of tree ages

Interpretation of forest disturbance history and a species regeneration pattern is frequently based upon the analysis of post-disturbance age-class distributions (Lorimer 1985). Reverse "j" shaped, unimodal and multimodal distributions of tree ages are characteristically interpreted as indicating continuous, catastrophic and gap-phase modes of regeneration (Veblen 1992). In particular even-aged stands are frequently interpreted as compelling evidence of infrequent episodic disturbance events (Oliver & Larson 1990; Veblen 1985).

Such age-class distributions can be erroneously interpreted, e.g., a stand may be mistakenly interpreted as even-aged if the age distributions of patches overlap due to the presence of trees from more than one patch in the study plot (Duncan & Stewart 1991). Conversely an uneven age-class structure does not necessarily indicate that a stand did not develop in the aftermath of a catastrophic disturbance event. A normal age distribution could result from several past circumstances; a single massive disturbance or slow recolonisation of a disturbed site (Lorimer 1985). Lorimer suggests various physical, physiological and structural forms of evidence to provide supporting evidence of disturbance history.

Due to the difficulty in accurately interpreting age-class distributions more detailed analysis was made by using the spatial distribution of tree ages. The presence of spatial structure within the three main stands was identified following the methods of Duncan and Stewart (1991). This approach relies on

the detection of spatial autocorrelation of the variable tree age. Spatial autocorrelation is a property mapped data possesses whenever it exhibits an organised pattern (Upton & Fingleton 1985). A variable is said to be autocorrelated when it is possible to predict the values of the variable at some points of space (or time) from the known value at other sampling points where spatial (or temporal) positions are also known (Legendre & Fortin 1989). (Classical inferential statistics cannot be used here because of the lack of independence of observations).

The method uses Moran's I to detect if neighbouring trees are of similar age. This was tested against the null hypothesis of total randomisation of the spatial distribution of the variate tree age.

Neighbouring points were defined from 3m distance classes. For each distance class a pair of trees i and j were considered neighbours if the distance between them was within the limits of distance class d. Morans coefficient I was calculated for each distance class as a measure of spatial autocorrelation, up to the length of the longest plot side.

$$I(d)=\frac{N\sum_{i}\sum_{j}W_{ij}v(x_i-\bar{x})(x_j-\bar{x})}{W\sum_{i}(x_i-\bar{x})^2}$$

$I(d)$	is the value of Moran's coefficient for distance class d
N	is the total number of point locations
Xi	(i =1,.....,N) is the value of the variate at each of N point locations
Wij=	equals 1 if points i and j were neighbours in distance class d, and 0 otherwise
$W=\sum W_{ij}$	

The significance of each autocorrelation value is tested against that expected from a random

distribution. Significant deviations from expected for each distance class are obtained by calculating the variance of I(d), using equations in Upton & Fingleton (1985, p171, eq 3.29). For each distance class standard normal deviates were computed.

A corellogram was constructed of the autocorrelation values that were plotted on the Y axis, against distance class (d) among localities on the X axis. Before examining each significant value a global test of significance was performed to ensure at least one value was significant at the general significance level α=0.05 (Legendre & Fortin 1989). This test is required because the significance tests for autocorrelation coefficients for each distance class do not provide a test of significance for the data set as a whole because the k tests are not independent (Sakai & Oden 1983). The number of distance classes were divided by 0.05 to give a new level of significance. The corellogram was globally significant if any of the new Z(d) values were significant at the new level. The null hypothesis for the corellogram is that the coefficient is not significantly different from zero.

Each corellogram was analysed by interpreting its shape, since characteristic shapes are associated with different types of spatial structures (Legendre & Fortin 1989). If trees occur in even-aged patches then a corellogram of tree age should show positive autocorrelation in small distance classes, reflecting the association of similar aged trees within a patch.

To determine the individual members of even-aged patches of trees suggested by the significant positive autocorrelation a measure of association was calculated C_{ij} (Duncan & Stewart 1991). This reflects both spatial proximity and tree age similarity between each pair of trees (Cliff et al. 1975). Values were calculated with a weighting of 0.5 giving distance and age equal weighting in the equation:

$$C_{ij}=\lambda\frac{d_{ij}}{d_{max}}+(1-\lambda)\frac{a_{ij}}{a_{max}}$$

a_{ij} and d_{ij}	are the differences in age, and distances between trees i and j, respectively
a_{max} and b_{max}	are the greatest age difference, and greatest distance between a pair of trees, respectively.
λ	is a constant ($0 \leq \lambda \leq 1$) that reflects the relative weighting assigned to distance versus age.

Non metric multidimensional scaling as implemented in the package PATN (Belbin 1989) was used to arrange trees in two dimensions from the matrix of association values. Also agglomerative hierarchical clustering (in the same package) was used to group trees of similar age and spatial proximity from the matrix of association values. This approach was developed by Duncan & Stewart (1991). If groups were spatially discrete and possessed a relatively even-aged age-class frequency distribution they were accepted as representative of even-aged groups.

6.2.8 Gap characteristics

Here the effects of disturbance are examined in more detail by determining patterns of tree mortality across the terraces, and the subsequent forest regeneration in the gaps. Different patterns of tree mortality between species can cause compositional shifts changing the relative abundance of canopy species, while gap size has often been viewed as the most important parameter determining which species regenerates. Unfortunately gaps could not be assessed across terrace 1 because of logging effects, nor could regeneration be assessed in the human induced gaps because of soil damage, where the subsequent water logging had generally prevented further regeneration of any tree species.

Two line transects were located on each terrace 100m apart parallel to the terrace edges. The first transect was located a random distance in from the terrace edge. Each gap (> $30m^2$) that the transect bisected was measured until a total of nineteen gaps were measured on terrace 2 and sixteen gaps on terrace 3. Ten gaps were sampled on the first transect and the remainder on the second. For each gap the area in canopy gap and expanded gap was measured (sensu Runkle

1982). The canopy gap was delimited by vertically projecting the opening in the canopy to the ground surface. The expanded gap included the canopy gap plus the adjacent area extending to the base of the surrounding trees. Individual areas of canopy gaps and expanded gaps were calculated by fitting their lengths L (longest distance from gap edge to gap edge) and widths W (longest distance at right angles to the length) to the formulae of an ellipse ($A=\pi LW/4$), which best described gap shape. For each tree that had made a canopy gap or expanded a canopy gap, diameter at breast height (1.3m) and type of damage (uprooted, standing dead, bole snap) was recorded. Regeneration in each treefall gap was determined by counting all seedlings and saplings of the conifer species, and from measuring the diameter of all trees $\geq$5cm dbh within the expanded gap area. Seedlings and saplings of *Weinmannia* and *Quintinia* were not counted because they were frequently too numerous to accurately assess. The light environment of different sized gaps was compared to levels of regeneration by computing the diameter/height (d/h) ratio for each gap (h= canopy height of trees adjacent of the gap). The average of canopy gap width and length was used to determine gap diameter. A higher d/h ratio implies better light conditions for regeneration. Gaps could not be aged by dating growth releases in annual ring-width increment because of ring wedging and lobate growth etc (See chapter 3).

6.2.9 Soil profile descriptions

The vegetation pattern in Westland is intimately linked with soils and landform (Chavasse 1971; Norton 1991). Soils typically vary between landforms reflecting geological and topographic variation. However, soils can also vary between similar landforms, such as glacial or river terraces where there is little topographic variation. Such variation generally reflects stage of soil development reflecting landform age (Smith & Lee 1984; Sowden 1986).

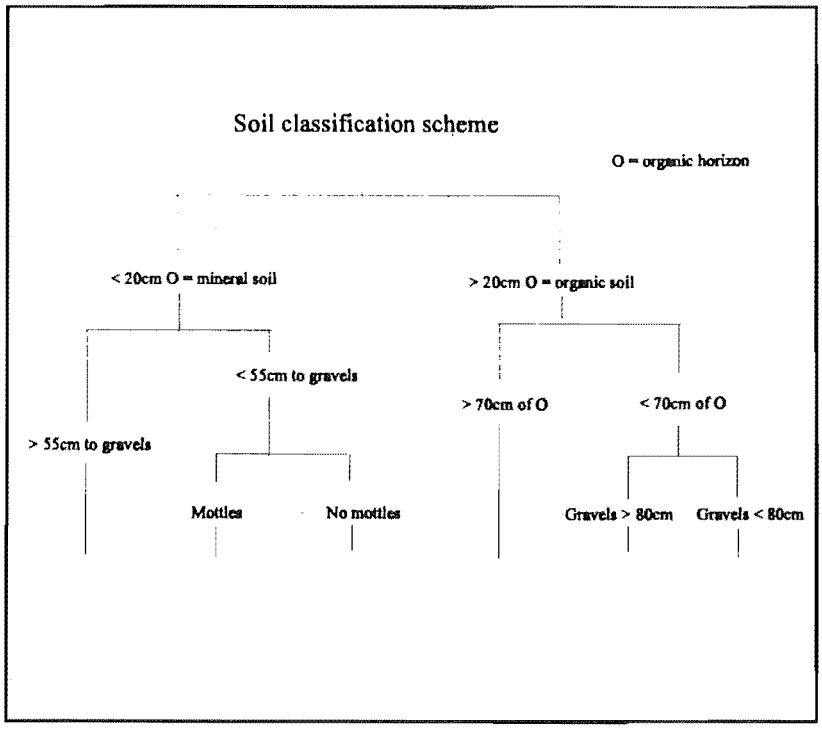
Soils show important changes in texture and structure and related properties with increasing depth effecting their capacity to store water and minerals and therefore their ability to support root and subsequent plant growth. In addition, variation in soil characteristics can effect patterns of structural

root growth and soil resistance to mechanical forces which effect a trees stability (Schaetzl et al. 1988). Successive changes in soil development can be determined in the field from soil morphological features. The more obvious changes are the vertical sequence and the relative thickness of soil horizons. These morphological changes reflect changes in soil chemistry and mineralogy (Tonkin et al 1985).

Here a rapid method of soil description was used because of the large number of samples. Fifty two soil descriptions of morphological features of the soils were made for each of the 0.4ha plots. Soils were sampled at the intersections of the 5m×5m quadrats by use of an auger, down to 1m depth and were described at 10m intervals. Descriptions were made based on the standard soil survey method for New Zealand (Taylor & Pohlen 1970). The main features of the soil horizons described were depth, deformability, strength, texture, the presence of mottles and the depth to gravels. Soils were then classified into six profile classes based upon their gross features, in a hierarchical scheme (Figure 6.1). The initial groups at the top of the hierachy were chosen to reflect major differences in stage of soil development. These major divisions were then increasingly defined further down the hierachy to reflect more subtle differences. The features were subjectively chosen based on characteristics that reflect differences in stage of soil development and factors that would effect the rooting environment. More precise definition of the stage of soil development can be achieved by the combination of field and laboratory data (Tonkin et al 1985), however laboratory analysis is time consuming and was impractical considering the sample numbers used here.

Soils were initially split into two groups based on whether they were predominantly organic (> 20cm depth of O horizon) or mineral soils. The mineral soils were then grouped according to the depth to gravels and whether they possessed mottles or not. The organic soils were classified according to the depth of the organic horizon and depth to gravels. For each plot the mean depth to gravels was calculated for the different profile classes.

Figure 6.1: Dendrogram of the hierarchical soil classification scheme



6.2.10 Soil drainage characteristics

Measurements of soil drainage in the lowland forests of south Westland have generally confined themselves to subjective classification schemes (Norton & Leathwick 1990; Duncan et al 1990). Subjective classification schemes generally categorise soil drainage into one of three relative classes, good, medium or poor based on the speed of run-off and degree of accumulation (internal drainage). However, in this study sites were generally flat so that degree of accumulation was the most appropriate measurement, which for such poorly drained soils could be reflected by the water table level.

Elsewhere relatively simple monitoring devices have been used to measure the water table depth as a measure of soil drainage. Boggie (1977) used a simple device using a float chamber to record maximum and minimum water table levels, while Lieffers & Rothwell (1987) used 5cm diameter perforated plastic tubing inserted at the sampling points from which measurements of the water table

depth could periodically be measured. However, in this present study mild steel rods were used to determine drainage, a method developed to determine oxygen restriction in soils prone to waterlogging. This technique is of general application to acidic soils because of the iron oxidation reaction which produces colour changes in the steel rods that indicate the aerobic depth. For this study the method was ideal in that it was cheap, quick to implement and required no monitoring and had been successfully used by Norton (1994) to determine drainage between different topographic locations in near by Ianthe Forest.

For the three main plots fifty two mild steel rods were located at 10m intervals across each at the points where soils had been sampled. In addition a further nine mild steel rods were located at regular intervals across three of the 40m×40m (Chapter 5) plots to determine whether stand variation within terraces, between stands dominated by large *Dacrydium* and those dominated by dense but smaller diameter *Dacrydium* and *Lagarostrobos* reflected soil drainage differences. The rods were left for four months between September 1993 and January 1994. Rainfall shows little seasonal fluctuation based on records from HariHari (N.Z. Met. Ser. 1983) so soil drainage is likely to be similar all year round. Measurement was made from the ground surface to the end of the point of rusting on each rod which indicated the aerobic depth (Carnel & Anderson 1986). The mean aerobic depth was calculated for each plot and for the soil profile classes in each plot.

6.3 Results

6.3.1 Composition and vertical structure of stands S1, S2 and S3

To compare the vertical structure of the main stands, data on the distribution of stems of the common tree species in the different relative height classes, from 1, shrub layer to 6, emergent layer are presented (Table 6.1)

Stand S1

Numerous stems of *Dacrydium* and *Lagarostrobos* dominated this stand, while *Prumnopitys* was uncommon. *Dacrydium* and *Lagarostrobos* made up 66% and 29% of the stems in the upper strata respectively (lower canopy, upper canopy and emergent strata). Many dead standing *Lagarostrobos* stems were present (123 stems ha^{-1}). Occasional *Prumnopitys* and *Quintinia* were present in the lower canopy. Subcanopy and understorey strata consisted mainly of small diameter *Weinmannia*. Stems of *Podocarpus hallii* (25 stems ha^{-1}), *Griselinia littoralis* (5 stems ha^{-1}), *Pseudopanax crassifolius* (3 stems ha^{-1}) and *Elaeocarpus hookerianus* (35 stems ha^{-1}) were present as minor tree species (≥ 5cm dbh). *Phyllocladus alpinus* was present only as seedlings and saplings.

Stand S2

Stems of *Dacrydium* were abundant from the understorey to emergent strata and dominated the upper canopy. In the lower strata, *Prumnopitys*, *Weinmannia* and *Quintinia* were abundant. A distinctive feature of stand S2 was the large number of stems of *Quintinia* in the subcanopy and the high stem density of *Phyllocladus alpinus* in the understorey of which many were dead or dying (250 stems ha^{-1}). In contrast to stand S1 *Lagarostrobos* was uncommon. *Elaeocarpus hookerianus* (28 stems ha^{-1}) and *Pseudopanax crassifolius* (23 stems ha^{-1}) were present as minor tree species.

Stand S3

Stand S3 was dominated by tall large diameter *Dacrydium cupressinum* (up to 110cm dbh). In the

upper three strata 92% of all stems were *Dacrydium*. The subcanopy was dominated by *Prumnopitys* stems (41%) and *Weinmannia* (36%). The conifers *Lagarostrobos colensoi*, *Phyllocladus alpinus* and *Dacrycarpus dacrydiodes* were rare. Other tree species present (≥ 5cm dbh) included *Quintinia acutifolia*, *Pseudopanax crassifolius* (3 stems ha^{-1}), *Myrsine australis* (28 stems ha^{-1}), *Elaeocarpus hookerianus* (3 stems ha^{-1}) and *Griselinia littoralis* (3 stems ha^{-1}). The stand possessed three distinct gaps formed from the windthrow of single large *Dacrydium* trees.

6.3.2 Population structure of the main species in stands S1, S2 and S3

For *Dacrydium* and *Lagarostrobos* in stand S1 the absence of *Dacrydium* saplings and paucity of *Lagarostrobos* saplings (Table 6.2), together with the low stem numbers in size-class 5-14cm dbh (Figure 6.2) suggests a discontinuous regeneration pattern, where regeneration had been more abundant in the past. The numerous seedlings of *Dacrydium* and absence of saplings suggests that the seedling population was ephemeral or was able to withstand lengthy periods of suppression. For *Prumnopitys* the absence of saplings and the paucity of stems suggests conditions had been unfavourable for regeneration, or alternatively this may be explained by a higher past mortality of established stems. Stems of *Dacrydium* ($310ha^{-1}$) were three times more abundant than stems of *Prumnopitys* ($108ha^{-1}$) and ten times more abundant than stems of *Lagarostrobos* ($30ha^{-1}$).

In stand S2 seedlings and saplings of *Dacrydium* and *Prumnopitys* were plentiful while *Lagarostrobos* saplings were uncommon. For *Dacrydium* the generally progressive decline in larger size-classes up to 64cm dbh followed by a marked increase suggests a sporadic regeneration pattern (Figure 6.2). For *Lagarostrobos* the paucity of saplings and the presence of only twelve stems also suggests sporadic regeneration had occurred. In contrast, for *Prumnopitys* the numerous seedlings and saplings and progressively fewer stems in larger size-classes up to 45cm dbh suggests a more continuous regeneration pattern. Stems of *Dacrydium* ($310ha^{-1}$) were three times more abundant than stems of *Prumnopitys* ($108\ ha^{-1}$) and ten times more abundant than stems of *Lagarostrobos* ($30ha^{-1}$)

Table 6.1: The number of trees ≥ 5cm dbh in relative height classes, stem density ha^{-1} and basal area m^2ha^{-1} for the main species in stands S1, S2 and S3. Class 1=shrub layer, 2=understorey, 3=subcanopy, 4=lower canopy, 5=upper canopy and 6=emergent layer.

species/class	1	2	3	4	5	6	Stem density No ha^{-1}	Basal area m^2ha^{-1}
Stand S1								
Dacrydium cupressinum	0	7	47	40	115	7	540	43.80
Prumnopitys ferruginea	0	3	5	1	0	0	23	0.65
Lagarostrobos colensoi	0	0	11	40	31	0	330	18.75
Weinmannia racemosa	2	113	87	0	1	0	513	4.35
Quintinia acutifolia	0	6	7	8	0	0	53	1.61
								Σ=69.16
Stand S2								
Dacrydium cupressinum	1	27	24	20	24	13	310	33.14
Prumnopitys ferruginea	0	17	23	3	0	0	108	4.40
Lagarostrobos colensoi	0	6	6	0	0	0	30	0.86
Phyllocladus alpinus	0	135	14	0	0	0	455	4.66
Weinmannia racemosa	0	129	37	1	0	0	418	5.27
Quintinia acutifolia	0	17	81	5	0	0	258	10.41
								Σ=58.74
Stand S3								
Dacrydium cupressinum	0	1	14	22	67	1	263	54.94
Prumnopitys ferruginea	0	8	31	4	1	0	113	8.54
Lagarostrobos colensoi	0	0	2	0	0	0	5	0.40
Dacrycarpus dacrydiodes	0	0	0	1	2	0	0	1.06
Phyllocladus alpinus	0	0	1	0	0	0	3	0.06
Weinmannia racemosa	2	194	27	0	0	0	558	7.15
Quintinia acutifolia	0	36	1	0	0	0	93	0.68
								Σ=72.83

Figure 6.2: Size-class frequency distributions for *Dacrydium cupressinum* and *Lagarostrobos colensoi* in stand S1, *Dacrydium cupressinum* and *Prumnopitys ferruginea* in stands S2 and S3 and *Phyllocladus alpinus* in stand S2. Size-classes are 10cm intervals beginning at 5-14cm dbh. n = number of trees in the stand.

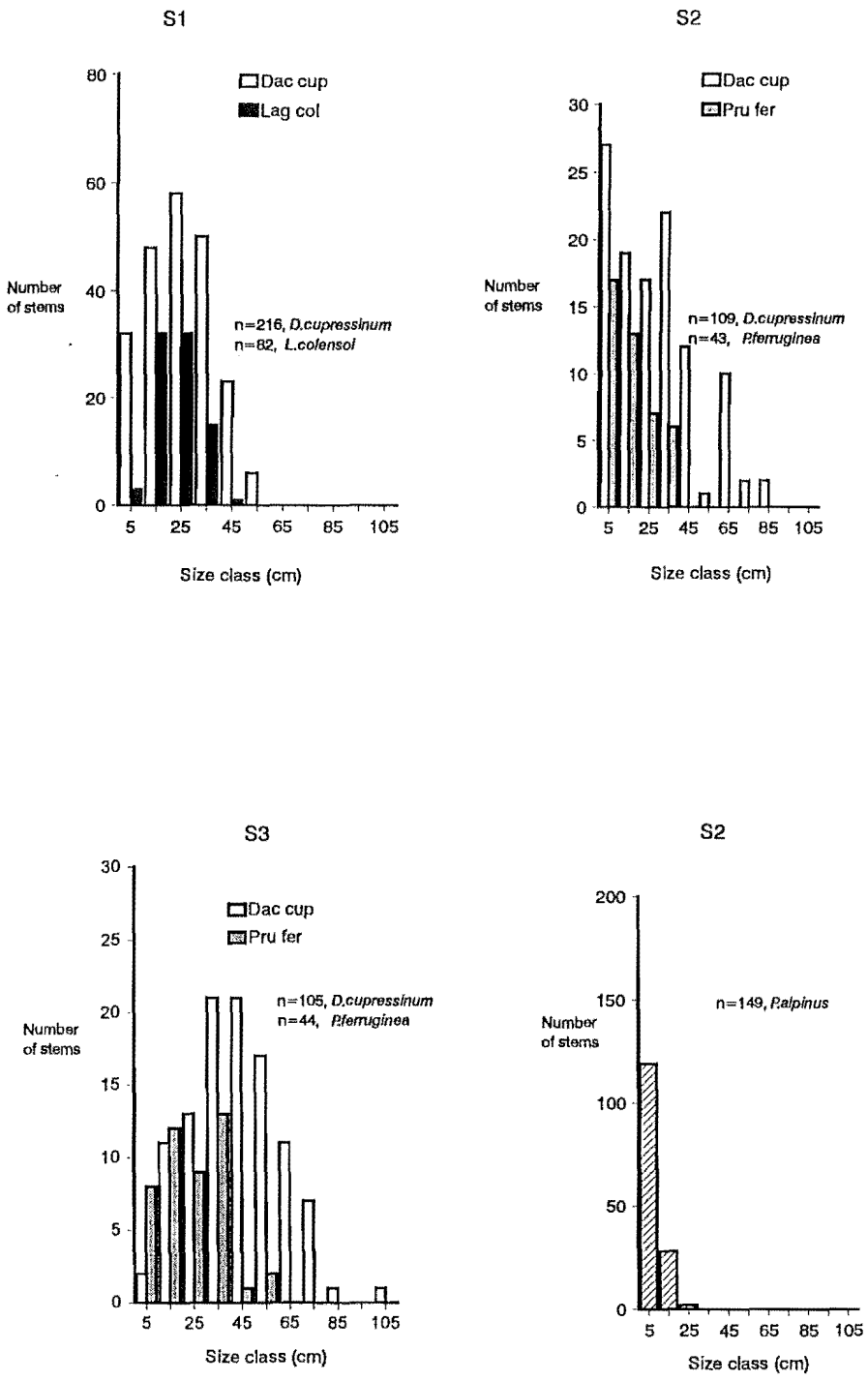
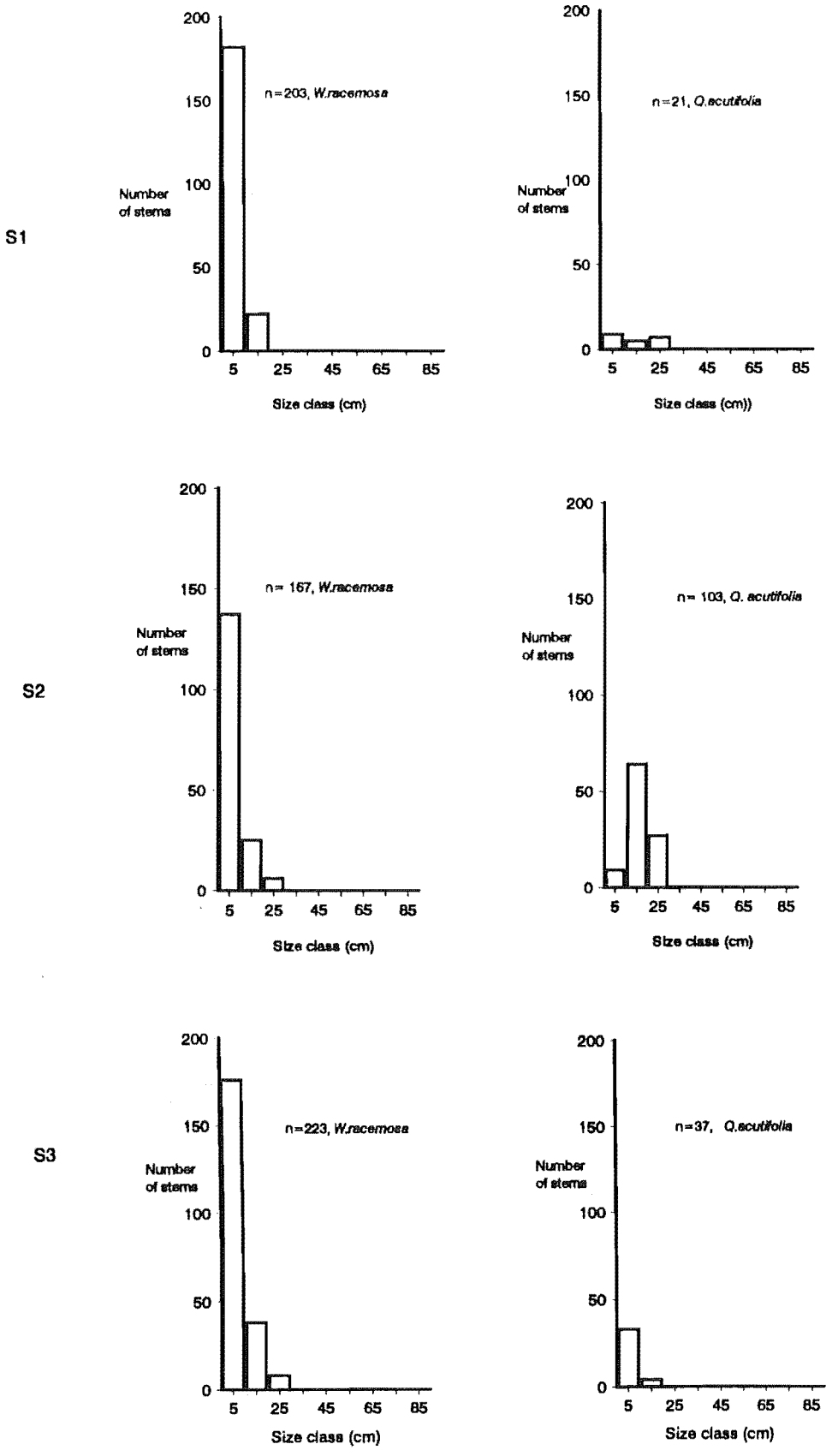


Figure 6.3: Size-class frequency distributions for *Weinmannia racemosa* and *Quintinia acutifolia* in stands S1, S2 and S3. Size classes are 10cm intervals beginning at 5-14cm dbh. n= number of trees in the stand.



In stand S3 the low numbers of saplings of *Dacrydium* and the unimodal distribution of stems in larger size-classes up to 105cm dbh suggests a discontinuous pattern of regeneration, as for *Dacrydium* in stand S1. For *Lagarostrobos* the moderate levels of seedlings and saplings and the scarcity of *Lagarostrobos* stems suggests conditions had either been unfavourable for growth to maturity or *Lagarostrobos* was starting to find conditions more favourable, alternatively mortality of previously established stems had been high. For *Prumnopitys* in contrast to stand S2, the numerous seedlings and saplings and the uneven distribution of stems in larger size-classes up to 65cm dbh suggests a more sporadic regeneration pattern. Stems of *Dacrydium* and *Prumnopitys* were largest in this stand reaching 105cm and 62cm dbh respectively. *Dacrydium* stems ($263ha^{-1}$) were c. two times more abundant than *Prumnopitys* stems ($113ha^{-1}$).

For *Phyllocladus* the numbers of seedlings and saplings and the distribution of stems in different size-classes indicated significant variation in the population structure between stands. In stand S1 seedlings and saplings were abundant, however stems of *Phyllocladus* were absent suggesting a failure of recruitment of individuals into adult size classes, or recent entry to the site. However, in stand S2 the numbers of seedlings and saplings and the progressively fewer stems in larger size-classes up to 35cm dbh suggests a more continuous regeneration pattern, while in stand S3 the absence of seedlings and scarcity of stems suggests a discontinuous regeneration pattern.

For *Weinmannia* in stand S1, in contrast to the discontinuous regeneration pattern of *Dacrydium* and *Lagarostrobos* the reverse 'j' shaped size-class frequency distribution (maximum size of 24cm dbh) (Figure 6.3), together with the abundant seedling and sapling population suggests a continuous regeneration pattern. Only 21 *Quintinia* trees were recorded having a maximum size of 31cm dbh. However 70% of the *Quintinia* stems were 18cm dbh or larger suggesting a predominantly old population of established trees despite the large number of seedlings and saplings. This suggests a discontinuous regeneration pattern. Stems of *Weinmannia* were ten times more abundant than stems of *Quintinia*.

For stand S2 the population structures of *Weinmannia* and *Quintinia* suggest contrasting regeneration patterns. The size-class frequency distribution of *Weinmannia* suggests a continuous regeneration pattern, while the unimodal size-class frequency distribution for *Quintinia* suggests a discontinuous regeneration pattern (Figure 6.3), which could reflect gap-phase regeneration. Only 9% of the *Quintinia* stems were less than 15cm dbh which implies the trees were predominantly older. Although *Weinmannia* stems were more abundant than *Quintinia*, the subcanopy had two times more *Quintinia* than *Weinmannia* stems suggesting conditions were more favourable for growth to maturity for *Quintinia* than *Weinmannia*.

For stand S3 *Weinmannia* stems were six times more abundant than *Quintinia*. The reverse "j" shaped size-class frequency distribution of *Weinmannia* stems suggests a continuous regeneration pattern. *Quintinia* stems were mainly small, with only 11% of stems > 15cm dbh which suggests that either larger trees have died or alternatively few stems have grown to a mature size, or that conditions have only recently become favourable for growth to maturity.

Table 6.2: Density (# ha^{-1}) of seedlings and saplings for the main tree species in stands S1, S2 & S3.

		Species					
Stand		*Dacrydium cupressinum*	*Lagarostrobos colensoi*	*Prumnopitys ferruginea*	*Phyllocladus alpinus*	*Weinmannia racemosa*	*Quintinia acutifolia*
S1	Seedlings	205	705	140	12407	44030	20925
	Saplings	0	27	0	586	13146	6893
S2	Seedlings	95	110	690	16872	31688	18106
	Saplings	103	3	160	133	2868	2533
S3	Seedlings	115	240	490	0	21573	13993
	Saplings	13	20	40	148	4493	2560

6.3.3 Conifer tree age/diameter relationships

For *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Phyllocladus alpinus* a significant relationship existed between age and diameter at breast height (Table 6.3). However age diameter relationships were poor for *Dacrydium* (Figure 6.4), compared to *Prumnopitys* (Figure 6.5),

particularly for *Dacrydium* in stand S1. In stand S2 the age diameter relationship for *Dacrydium* over the first c. 170 years was better than after this period (Figure 10). Trees older than this had a more variable diameters for a given age. The spread of ages for a given diameter was greatest in stand S2, where age range increased with diameter while in stand S1 the spread of ages was much less. For example the age range at 40cm dbh was c. 125 years for stand S1, 300 years for stand S2 and 270 years for stand S3. This suggests a more uniform growing environment for *Dacrydium* in stand S1.

Prumnopitys ferruginea and *Phyllocladus alpinus* had linear age/diameter relationships for the given age range which suggests they were less affected by changes in their environment (e.g. lighting) once established, compared to *Dacrydium* (Figure 6.5). For *Lagarostrobos* in stand S1 no regression model could be adequately fitted to the data because of the lack of a significant relationship between age and diameter. This was reflected in the uniformity of *Lagarostrobos* stems. Of the *Lagarostrobos* stems in stand S1, 75% were between 15cm and 34cm dbh (range 11 to 52cm) and 87% of the stems were in the lower and upper canopy classes.

Table 6.3: Best fit regression equations for estimating tree age in years (Y) from diameter at breast height (X) for *Dacrydium cupressinum*, *Lagarostrobos colensoi*, *Prumnopitys ferruginea* and *Phyllocladus alpinus* and mean annual ring width increment (mm yr^{-1}). n=sample number.

Stand	Species	Regression equation	r^2	Mean annual ring width increment (mm yr^{-1})	n	p
S1	*Dacrydium cupressinum*	$\log_e Y=5.6-7.6\times 1/X$	0.54	0.7 ± 0.3	191	0.0001
	Lagarostrobos colensoi			0.6 ± 0.1	50	
S2	*Dacrydium cupressinum*	$Y=92.82+7.1031X$	0.52	0.6 ± 0.3	90	0.0001
	Prumnopitys ferruginea	$Y=87.7077+7.1031X$	0.81	0.4± 0.1	34	0.0001
	Phyllocladus alpinus	$Y=13.6+11.1X$	0.87	0.4±0.1	26	0.0001
S3	*Dacrydium cupressinum*	$\log_e Y= -72.2746+107.4455 \log_e X$	0.32	0.7± 0.4	94	0.0001
	Prumnopitys ferruginea	$\log_e Y=3.021568+0.784690 \log_e X$	0.81	0.4± 0.1	76	0.0001

Figure 6.4: Age diameter relationship for *Dacrydium cupressinum* in stands S1, S2, & S3.

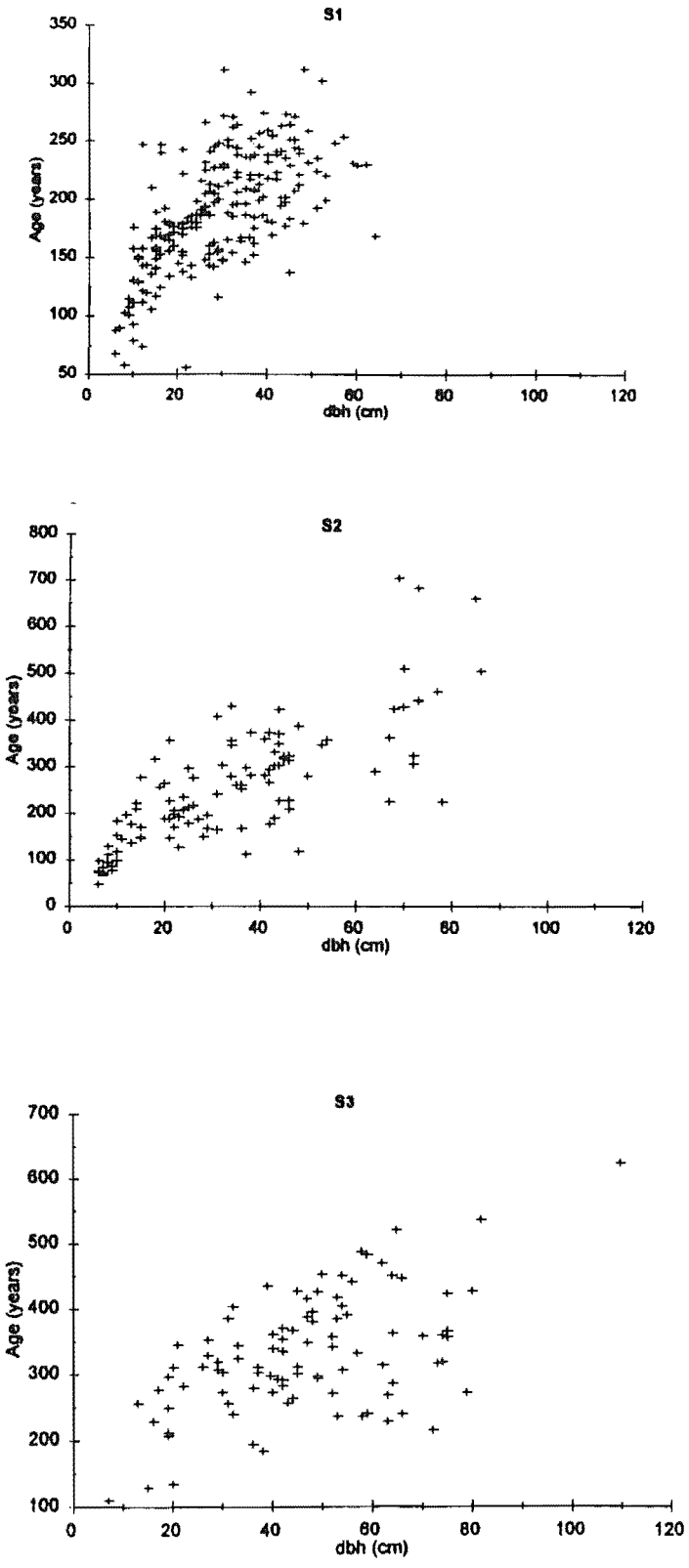
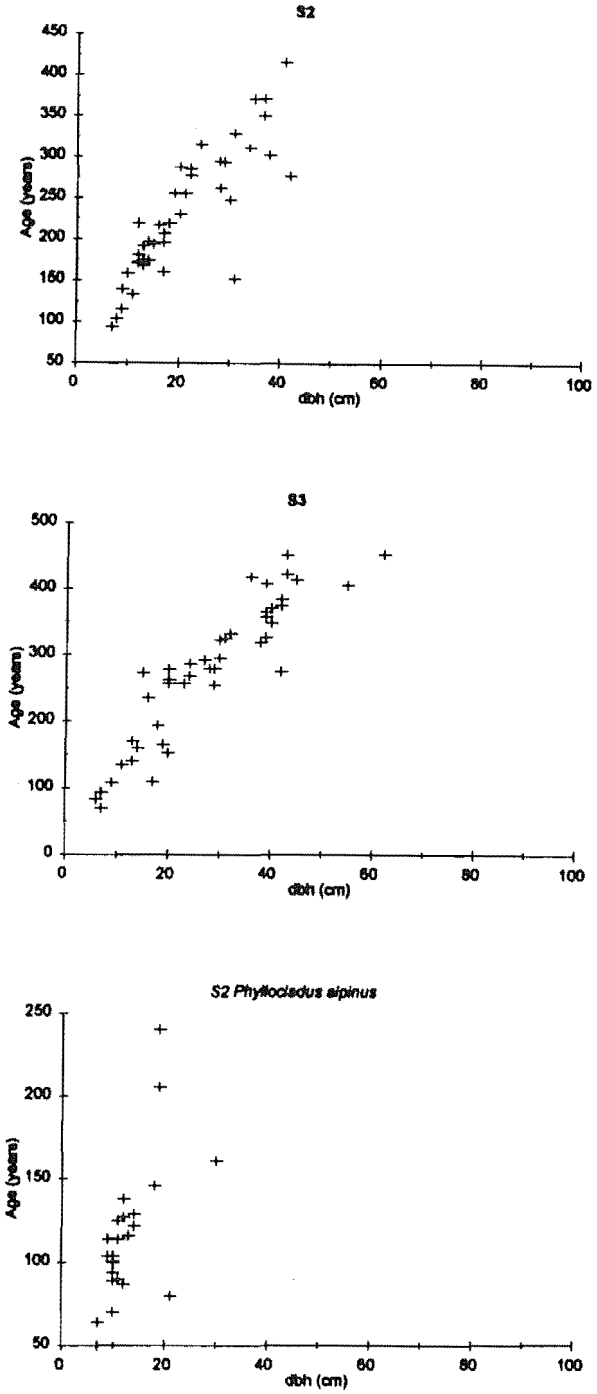


Figure 6.5: Age diameter relationship for *Prumnopitys ferruginea* in stands S2 & S3 and *Phyllocladus alpinus* in S2.



6.3.4 Population size and age-class structure for stand S1r

This stand was sampled to represent an early stage of development of stand S1. The stand was densely populated with *Dacrydium* saplings (41000 ha^{-1}) and small trees (18000 ha^{-1}), and small stems of *Phyllocladus alpinus* (15000 ha^{-1}). Establishment of *Dacrydium* seedlings had effectively ceased as few were present and all were > 50cm height. The size-class frequency distribution suggested establishment of *Dacrydium* had peaked (Figure 6.6). The ten cores taken from the small *Dacrydium* trees (6.0-22.7cm dbh) ranged from 85-138 years and the six cross sections taken from saplings (1.2-3.7cm dbh) indicated a range of 36 -105 years. This suggests establishment occurred over at least 102 years. This period could be longer if the current seedlings grow on to become mature trees. The four *Phyllocladus* trees aged were 106, 113, 125 and 148 years old suggesting contemporaneous establishment to *Dacrydium*.

6.3.5 Age-class frequency distributions for stands S1, S2 & S3

Stand S1

Dacrydium and *Lagarostrobos* possessed bell shaped size-class frequency distributions suggestive of an even-aged stand that established after catastrophic disturbance (Figure 6.6). For *Dacrydium* and *Lagarostrobos* the distribution of stems in age-classes up to 350 years indicated broadly even-aged populations of mean age 192 ± 49 years and 222 ± 38 years respectively. The main period of stand establishment for both species commenced 201-250 years ago. High levels of establishment of *Dacrydium* were maintained for 150 years. Establishment of *Lagarostrobos* effectively ceased 150 years ago coinciding with a substantial drop in establishment of *Dacrydium*. This could indicate the time when canopy closure prevented further *Lagarostrobos* establishment. The absence of any secondary peaks in the age-class frequency distributions suggests no further significant disturbance had affected the stand, or that any openings have been monopolised by the abundant seedlings and saplings of Weinmannia and Quintinia, preventing further conifer regeneration. The nine *Prumnopitys ferruginea* trees ranged in size from 8-25cm dbh and from 63-258 years suggesting a broadly even-aged population.

Stand S2

For *Dacrydium* the all aged frequency distribution indicated pulses of regeneration had occurred over the last 750 years, reflecting intermittent canopy gap formation. Establishment had consistently occurred over the last 450 years (Figure 6.6).

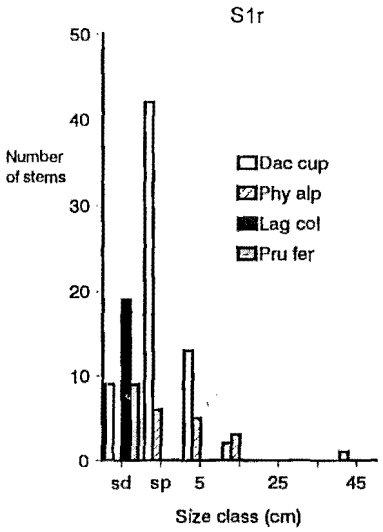
For *Prumnopitys ferruginea* the age-class frequency distribution suggested a more sporadic regeneration pattern than was suggested by the size-class frequency distribution (Figure 6.6). Initial establishment occurred c. 450 years ago, with above average establishment 151-200 years ago followed by a sharp decline from 150 years ago. Alternatively the age-class frequency distribution may be explained by a higher rate of mortality either side of this period. The concurrent peak establishment periods for *Dacrydium* and *Prumnopitys* presumably reflect establishment in response to the same disturbance event.

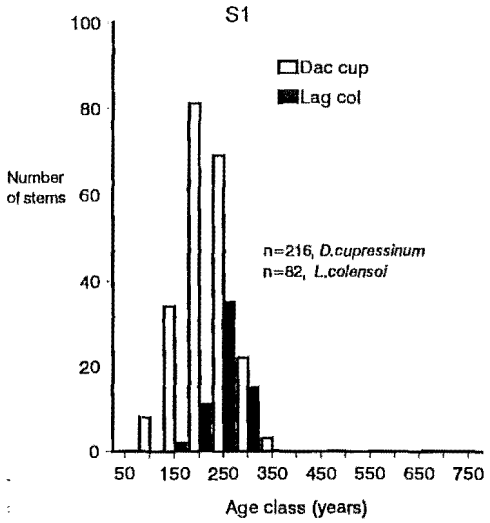
Lagarostrobos had a sporadic age structure with nine of the twelve stems present aged between 80 and 141 years old with two older trees of 300 and 448 years. For *Phyllocladus*, the most abundant species in the stand (455 stems ha^{-1}) the continuous regeneration pattern suggested by the size-class frequency distribution was not evident in the unimodal age-class frequency distribution which indicated that the trees were even aged (Figure 6.6). The main period of establishment commenced 101-150 years ago after the peak establishment of *Dacrydium* and *Prumnopitys*. This continued for a period of 100 years followed by a marked decline in establishment from 50 years ago until present.

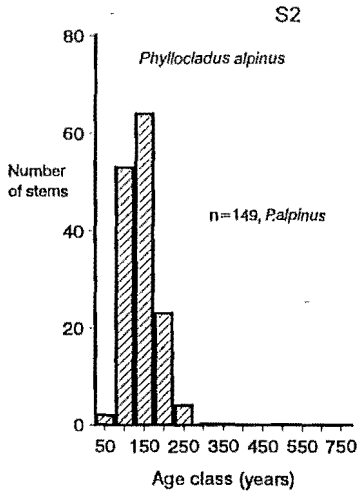
Stand S3

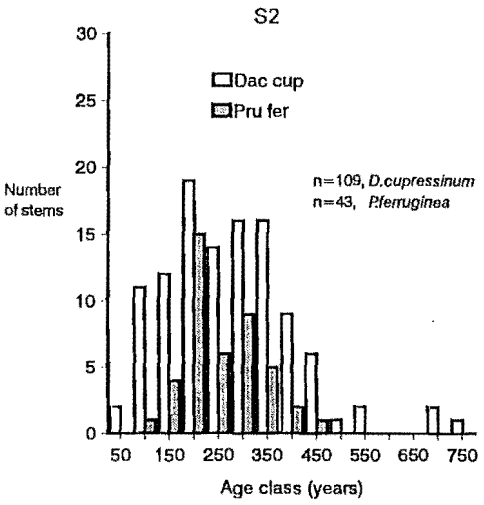
For *Dacrydium cupressinum* the bell shaped age-class frequency distribution (Figure 6.6) indicated the trees had established over the last 650 years. Higher levels of establishment occurred 251-400 years ago. Alternatively, this may be explained by higher levels of mortality either side of this period, 101-250 years ago and 401-650 years ago. No *Dacrydium* trees were present less than 100 years old which suggests closed canopy conditions had prevented further *Dacrydium* regeneration.

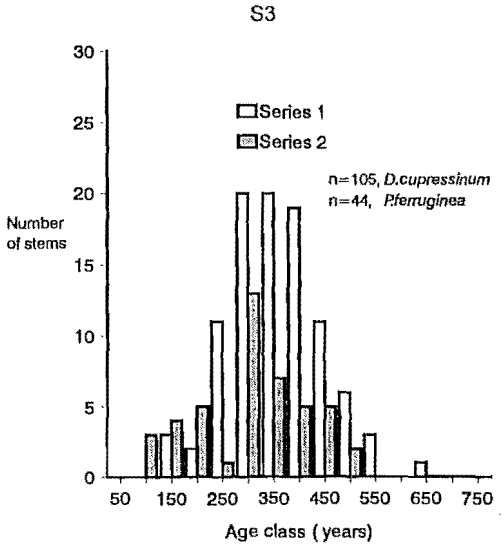
Figure 6.6: Size-class frequency distribution for stand S1r (Sd=seedlings, S=saplings). Size classes are 10cm intervals beginning at 5-14cm dbh. Age-class frequency distributions for *Dacrydium cupressinum* and *Lagarostrobos colensoi* in stand S1, *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Phyllocladus alpinus* in stand S2 and *Dacrydium cupressinum* and *Prumnopitys ferruginea* in stand S3. Age classes are 50 year intervals beginning at 1-50 years.











The age-class frequency distribution of *Prumnopitys ferruginea* suggests a sporadic pattern of regeneration had occurred over the past 500 years (Figure 6.6). Above average establishment occurred 251-300 years ago followed by a marked drop 201-250 years ago indicating the end of the establishment period, or an above average period of mortality. Other conifers present included one *Lagarostrobos colensoi* tree aged 262 years, one *Phyllocladus alpinus* tree aged 250 years and three *Dacrycarpus dacrydioides* trees aged 241, 246, and 273 years. The age of these trees coincides with the peak period of establishment of *Dacrydium* and *Prumnopitys* presumably reflecting the period of maximum canopy opening. The extensive period of establishment of *Dacrydium* and *Prumnopitys* suggests a progressive period of overstorey mortality had occurred.

6.3.6 Seedling and sapling establishment patterns

Seedlings overall were more abundant on the forest floor reflecting establishment site availability, however different patterns of establishment site preference were evident amongst species. The percentage of seedlings on different substrates in comparison to the percentage substrate availability suggested some species preferentially established on raised sites (Table 6.4). For all species except *Prumnopitys* and *Phyllocladus* raised establishment sites were preferred, particularly for *Dacrydium* and *Lagarostrobos*. In stand S1 seedlings of *Dacrydium* were exclusively found on logs while in stand S2 mounds and logs were favoured. *Lagarostrobos* also favoured mounds in stands S2 and S3 although seedlings were abundant on the forest floor. Although 100% of *Dacrydium* seedlings favoured logs in stand S1 there was no evidence to suggest that the present canopy trees had established on raised sites. However, it is unlikely that evidence of having established on a raised site such as a log would remain after 100 years or so.

Prumnopitys occasionally occurred on mounds and logs, with seedlings favouring mounds in stands S2 and S3. However, a greater percentage had established on the forest floor than either *Dacrydium* or *Lagarostrobos*. For the two stands in which *Phyllocladus* seedlings occurred (S1 & S2), the forest floor was favoured.

The percentage of seedlings of *Weinmannia* and *Quintinia* on different establishment sites in stand S1 occurred at similar levels to the percentage of different substrates available as reflected by the non significant distribution, however, in stands S2 and S3 raised substrates were favoured although seedlings were abundant on the forest floor. *Quintinia* favoured logs in stands S1 and S2 but mounds in stand S3. For *Weinmannia* in stand S2 mounds were favoured, while mounds and logs were favoured in stand S3.

Table 6.4: Percentage of seedlings found on log, mound, and forest floor for stands S1, S2 and S3. Numbers in brackets indicate % of establishment substrate encountered. n = sample number. Significant differences in the distributions of seedlings on establishment sites are indicated by an asterix reflecting establishment on sites more or less than would be expected than if they were distributed randomly (Chi squared test $P<0.05$).

Stand	Substrate	*Dacrydium cupressinum*	*Lagarostrobos colensoi*	*Prumnopitys ferruginea*	*Phyllocladus alpinus*	*Weinmannia racemosa*	*Quintinia acutifolia*
S1	Log (16%)	100	81	18	12	18	20
	Mound(20%)	0	4	3	3	16	16
	Floor (64%)	0	15	79	85	66	64
	n	42*	280*	28*	67*	238	113
S2	Log (5%)	16	25	3	7	1	16
	Mound (4%)	22	21	17	5	12	7
	Floor (91%)	63	54	80	88	87	77
	n	19*	24*	138*	41	77	44
S3	Log (13%)	80	22	16	0	20	18
	Mound(11%)	10	37	27	0	21	35
	Floor (76%)	10	41	55	0	59	47
	n	23*	48*	98*	0	74*	34*

Although seedlings may establish over a wide range of establishment sites only those on the most favourable establishment site would be expected to persist through to a sapling stage. Saplings of *Phyllocladus*, *Weinmannia* and *Quintinia* occurred most frequently on the forest floor (Table 6.5).

However, saplings of *Quintinia* favoured raised substrates and in particular mounds in stands S2 and S3. For *Quintinia* the higher percentage of saplings on the forest floor in stand S3 compared to the number of seedlings on the forest floor may reflect extensive suckering, and similarly for *Weinmannia* in all three stands. The distribution of *Phyllocladus* saplings in stand S1 suggested a preference for the floor, however in stand S2 and S3 the sample number was too small to confidently interpret the result.

Table 6.5: The percentage of saplings found on, log, mound and forest floor for stands S1, S2 & S3. Numbers in brackets indicate % of establishment substrate encountered. n = sample number. Significant differences in the distributions of saplings on establishment sites are indicated by an asterix reflecting establishment on sites more or less than would be expected than if they were distributed randomly (Chi squared test $P<0.05$).

Stand	Substrate	*Phyllocladus alpinus*	*Weinmannia racemosa*	*Quintinia acutifolia*
S1	Log (16%)	7	9	9
	Mound (20%)	14	5	23
	Floor (64%)	79	86	68
	n	44	986*	517
S2	Log (5%)	12	2	2
	Mound (4%)	44	11	26
	Floor (91%)	12	87	72
	n	10*	215	190*
S3	Log (13%)	0	6	11
	Mound (11%)	0	11	21
	Floor (76%)	100	83	68
	n	11	337	192*

6.3.7 Seedling canopy cover light environments

The percentage of different overhead canopy cover classes sampled suggested that in all three stands more closed canopy conditions were prevalent (classes 4,5 & 6), with stand S1 having the least closed canopy (Table 6.6). However, the effect of any opening on seedling light environments

will depend on the height of the canopy and the tier structure, and the response of competing vegetation to this change.

In general the distribution of seedlings under different canopy covers significantly differed from that expected if they were distributed at random. For *Lagarostrobos* a higher percentage of seedlings was found below more open canopy cover conditions in stands S1 and S3 than for *Dacrydium*. This could reflect the less shade tolerant nature of *Lagarostrobos* compared to *Dacrydium*. This pattern was not evident in stand S2, which may reflect the low sample number. The distributions of *Prumnopitys* seedlings suggests a greater tolerance to more closed canopy conditions. In general a higher percentage was evident in canopy cover classes 5 and 6 compared to *Dacrydium* and *Lagarostrobos*.

Table 6.6: Percentage of conifer seedlings found below different levels of canopy cover (class 1 to 6 , 1=<1%, 2=1-5%, 3=6-25%, 4=26-50%, 5=51-75%, 6=76-100%) for stands S1, S2 and S3. % cover classes = percentage of each cover class sampled. Significant differences in the distribution of seedlings below different levels of canopy cover are indicated by an asterix and reflect a significantly different distribution than would be expected if the seedlings were randomly dispersed (Chi-squared test $P < 0.05$). n=sample number.

		Cover class						
Stand		**1**	**2**	**3**	**4**	**5**	**6**	**n**
S1	*Dacrydium cupressinum* *	15	24	54	0	7	0	42
	Lagarostrobos colensoi *	42	2	52	3	1	0	280
	Prumnopitys ferruginea *	21	0	57	7	11	4	28
	% cover class	5	2	17	19	38	19	
S2	*Dacrydium cupressinum* *	0	0	21	42	26	11	19
	Lagarostrobos colensoi	0	0	8	54	17	21	24
	Prumnopitys ferruginea	0	0	20	18	10	52	138
	% cover class	0	1	9	25	18	47	
S3	*Dacrydium cupressinum* *	0	0	8	69	21	0	23
	Lagarostrobos colensoi *	0	0	45	22	20	10	48
	Prumnopitys ferruginea *	0	0	15	30	36	16	98
	% cover class	1	0	9	20	29	41	

6.3.8 Spatial pattern of individual species and species associations

The next two sections present evidence of significant spatial relationships for the main species in each stand. Section 6.3.8 deals with the spatial distributions and associations between pairs of species. Section 6.3.9 looks specifically at the spatial distribution of tree ages, presenting evidence on different types of spatial structure.

All species in each stand except *Quintinia acutifolia* in stand S2 had significant patterns of spatial

dispersion. Patterns of clumping at small scales for the conifer species were attributed to patchy establishment sites. Different scales of clumping for different species amongst stands were attributed to establishment in different sized disturbance openings.

The bivariate pattern of spatial dispersion indicated species interactions and patterns of establishment during stand development, also in stands S2 and S3 negative associations of different species coincided with disjunct distributions of differently drained soils.

Stand S1

Dacrydium cupressinum and *Lagarostrobos colensoi* (201-250 years) were clumped at similar scales suggesting a similar establishment response to a disturbance (Table 6.7). However *Dacrydium* and *Lagarostrobos* were negatively associated reflecting their spatial segregation within the plot (Figure 6.6). This may reflect patchiness in the environment at the time of establishment.

Small diameter *Weinmannia* were aggregated mainly at distances greater than 6m reflecting the presence of variable sized overlapping patches, possibly reflecting establishment in response to small and intermediate sized canopy openings (Figure 6.7). The clumped distribution of large *Weinmannia* (at 2m only) suggests that small patches of neighbouring trees were present which were randomly distributed. The positive association of small *Weinmannia* with *Dacrydium* 151-200 and 201-250 years old suggests *Weinmannia* was able to regenerate beneath the canopy of *Dacrydium* trees, but the non significant association of the larger stems with *Dacrydium* suggests this is not necessarily an establishment site in which they will reach maturity. The positive association of *Weinmannia* (≥15cm dbh) with *Lagarostrobos* (151-251 years) may be attributed to higher subcanopy light levels beneath the more diffuse canopy of *Lagarostrobos* (Table 6.8, Figure 6.7). A similar pattern was also evident for stems of *Quintinia* (≥15cm dbh).

Table 6.7: Patterns of spatial dispersion for trees (by species, age and size-class) in stand S1. Letters indicate significant (P < 0.05) deviation from a random distribution based on values of the function L (t); C denotes a clumped distribution, . denotes a random distribution. Only size-classes with > 10 individuals were analysed.

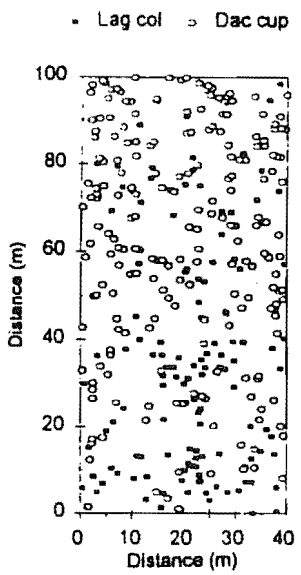
		Distance class (m)
Age-class (years)	Species	1 . . . 5 . . . . 10 . . . . 15 20
	Dacrydium cupressinum <150	. . C C C C C C C C C C C C C C C C C C C
	Dacrydium cupressinum 151-200	. C C C C C C C C C C C C C C C C C C C
	Lagarostrobos colensoi 151-200	. . . . .
	Lagarostrobos colensoi 201-250	C C C C C C C C C C C C C C C C C C C
Size-class (cm)	*Weinmannia racemosa* 5-14	. . C . . . C C C C C C C C C C C C C C
	Weinmannia racemosa ≥15	. C . . . . .
	Quintinia acutifolia ≥15	. . . . .

Table 6.8: Patterns of association for trees (by species, age and size-class) for stand S1 from the function $L_{12}(t)$. N & P denote significant (P < 0.05) negative and positive association at distances of up to 20m, R denotes no significant association. Only size-classes with > 10 individuals were analysed.

		Age-class (years)				Size-class (cm)		
Age-class (years)	Species	DC 151-200	DC <150	LC 201-250	LC 151-200	WR 5-14	WR ≥15	QA ≥15
	Dacrydium cupressinum 201-250	N	N	R	N	P	R	R
	Dacrydium cupressinum 151-200		P	N	N	P	R	N
	Dacrydium cupressinum <150			N	R	N	R	N
	Lagarostrobos colensoi 201-250				N	R	R	P
	Lagarostrobos colensoi 151-200					P	P	P
Size-class (cm)	*Weinmannia racemosa* 5-14						N	R
	Weinmannia racemosa ≥15							R

Figure 6.7: (a) Stem map showing the negative relationship between *Dacrydium cupressinum* and *Lagarostrobos colensoi* , (b) stem map of *Weinmannia racemosa* (5-14cm dbh) showing different scales of clumping in stand S1, and stem map showing the positive association of (c) *Quintinia acutifolia* (≥15cm dbh) and (d) *Weinmannia racemosa* (≥15cm dbh) with *Lagarostrobos colensoi* (151-200 years) in stand S1.

(a)



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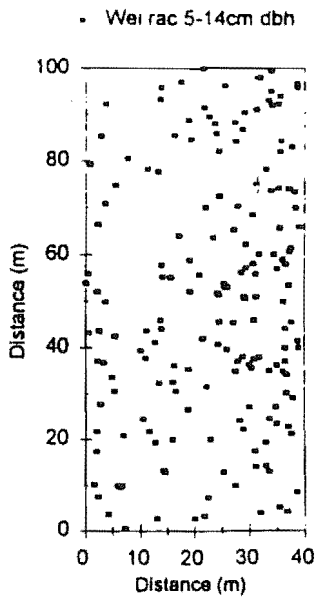

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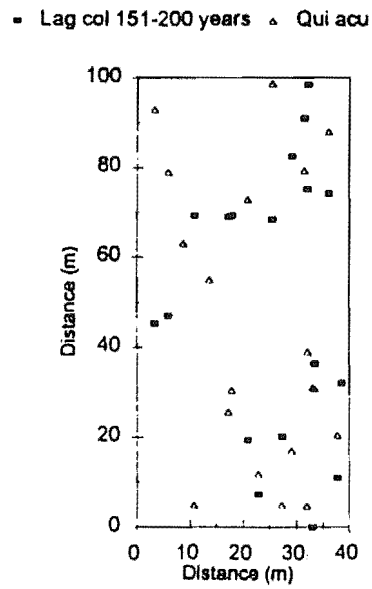

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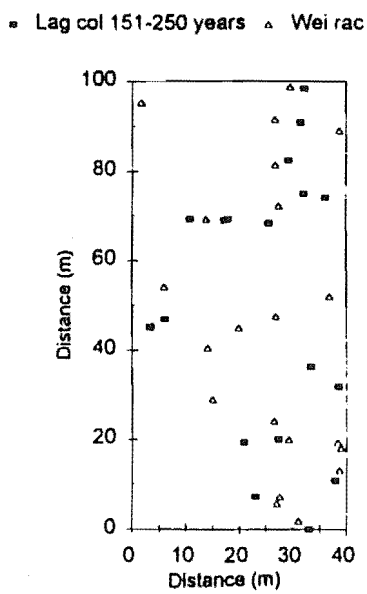


Stand S2

For *Dacrydium* small scales of clumping indicated the presence of small groups of similarly aged adjacent trees within the larger scale patches, reflecting establishment in disturbance openings. These different scales of clumping were also evident for *Phyllocladus*. *Quintinia* and *Weinmannia* were not clumped at such large scales. This reflected establishment in smaller scale canopy openings (Table 6.9). *Prumnopitys* (151-300 years old) was clumped at larger scales only, reflecting establishment in larger canopy openings.

The negative association of *Phyllocladus* with *Dacrydium* trees ≥ 150 years reflected establishment away from existing canopy and subcanopy trees while the negative association of *Phyllocladus* (≤150 years) with *Prumnopitys* reflected that the majority of trees of these two species were disjunctly distributed (Table 6.10a). *Phyllocladus* favoured the bottom half of the plot where the soils were most poorly drained (Figure 6.8). Large *Weinmannia*, although not significantly clumped indicated establishment with older *Dacrydium* (in contrast to *Weinmannia* in stand S1) and *Prumnopitys* stems which may reflect contemporaneous establishment. Small stems of *Weinmannia* indicated establishment with the younger (≥ 150 years old) stems of *Phyllocladus* away from those occupied by large *Weinmannia* (Figure 6.7).

Saplings of *Dacrydium* and *Prumnopitys* were clumped at small and large scales (Table 6.10b). *Dacrydium* saplings indicated establishment away from *Prumnopitys*, *Weinmannia* and *Quintinia* but were randomly dispersed in relation to parent trees, having established with *Phyllocladus* (Figure 6.7). *Prumnopitys* saplings occurred in smaller clumps than *Dacrydium*, indicated by significant clumping at scales of 2m. This was attributed to establishment in smaller canopy openings. The negative association with other species apart from *Phyllocladus* indicated regeneration away from established canopies and in particular parent trees (Figure 6.8). These patterns of spatial dispersion suggest that saplings of *Dacrydium* and *Prumnopitys* preferred more open sites.

Table 6.9: Patterns of spatial dispersion for tees (by species age-class and size-class) in stand S2. Letters indicate significant ($P < 0.05$) deviation from a random distribution based on values of the function L *(t)*; C denotes a clumped distribution, . denotes a random distribution. Only size-classes with > 10 individuals were analysed.

		Distance class (m)																			
Age-class (years)	Species	1	.	.	.	5	.	.	.	.	10	.	.	.	.	15	.	.	.	.	20
	Dacrydium cupressinum ≤150	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Dacrydium cupressinum 151-300	.	.	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	Dacrydium cupressinum saplings	.	.	.	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	.
	Dacrydium cupressinum >300	.	C	C	.	.	.	.	.	.	.	.	.	.	C	C	C	C	C	C	C
	Prumnopitys ferruginea 151-300	.	.	.	.	.	.	.	.	.	C	C	C	C	C	C	C	C	C	C	C
	Prumnopitys ferruginea saplings	.	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	Phyllocladus alpinus ≤150	.	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C
	Phyllocladus alpinus 151-300	.	.	.	.	.	.	.	.	.	.	.	.	C	C	C	C	C	C	C	C
Size-class (cm)	*Weinmannia racemosa* 5-14	.	.	.	.	.	.	.	.	.	C	C	.	.	.	.	.	.	.	.	.
	Weinmannia racemosa ≥15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
	Quintinia acutifolia ≥15cm	.	.	.	C	C	C	C	C	C	C	C	C	C	C	.	.	.	.	.	.

Table 6.10a: Patterns of association for trees (by species, size and age-class) in stand S2 from the function $L_{12}(t)$. N & P denote significant ($P < 0.05$) negative and positive association at distances of t up to 20m, R denotes no significant association. Only size-classes with > 10 individuals were analysed.

		Age-class (years)					Size-class (cm)		
		DC	DC	PF	PA	PA	WR	WR	QA
Age-class (years)		151-300	≤150	151-300	151-300	≤150	≥15	5-14	≥15
	Dacrydium cupressinum ≥300	P	N	P	R.	N	P	N	R
	Dacrydium cupressinum 151-300		P	R	N	N	P	R	R
	Dacrydium cupressinum ≤150			N	R	R	N	R	R
	Prumnopitys ferruginea 151-300				R	N	P	R	P
	Phyllocladus alpinus 151-300					P	N	R	R
	Phyllocladus alpinus ≤150						N	P	N
Size-class (cm)	*Weinmannia racemosa* 5-14							N	P
	Weinmannia racemosa ≤15								R

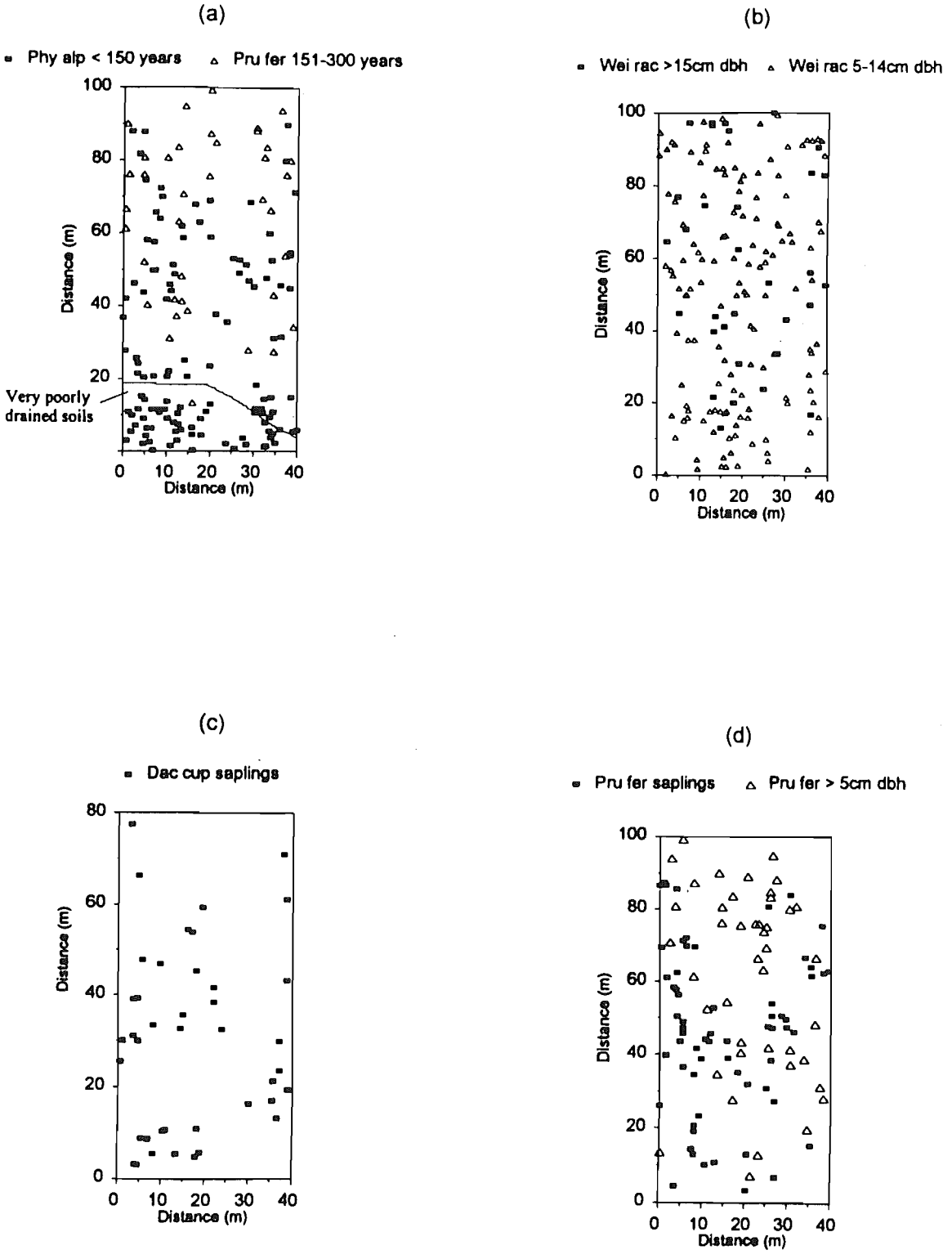
Table 6.10b: Patterns of association for trees and saplings (by species) in stand S2, from the function $L_{12}(t)$. + & - denote significant ($P < 0.05$) positive and negative association at distances of t up to 5m, R denotes no significant association. Figures indicate scale of association. Only size-classes with > 10 individuals were analysed.

Species	All Dac cup	All Pru fer	Wei rac 5-14cm	Wei rac ≥15cm	All Qui acu	All Phy alp
Dacrydium cupressinum	R	- 4	R	R	R	+4,5
Prumnopitys ferruginea	- 4	- 4	- 3 -5	R	- 4	R

Stand S3

Significant patterns of spatial dispersion indicated that both conifers and angiosperms were clumped at various scales (Table 6.11). Small scale clumping of the *Dacrydium* age group 301-450 years indicated the presence of small groups of adjacent neighbouring trees within the larger patch structure, indicated by significant clumping up to the 20m analysis limit. However, the 151-300 year group was not clumped at such large scales reflecting establishment in smaller scale canopy

Figure 6.8: (a) Stem map showing the disjunct locations of *Prumnopitys ferruginea* (151-300 years) and *Phyllocladus alpinus* (≤150 years) and the distribution of differently drained soils, (b) stem map showing the negative association between *Weinmannia racemosa* 5-14cm dbh and *Weinmannia racemosa* ≥15cm dbh, (c) stem map showing the clumped distribution of *Dacrydium cupressinum* saplings, and (d) stem map showing the disjunct distribution of trees and saplings of *Prumnopitys ferruginea* in stand S2.



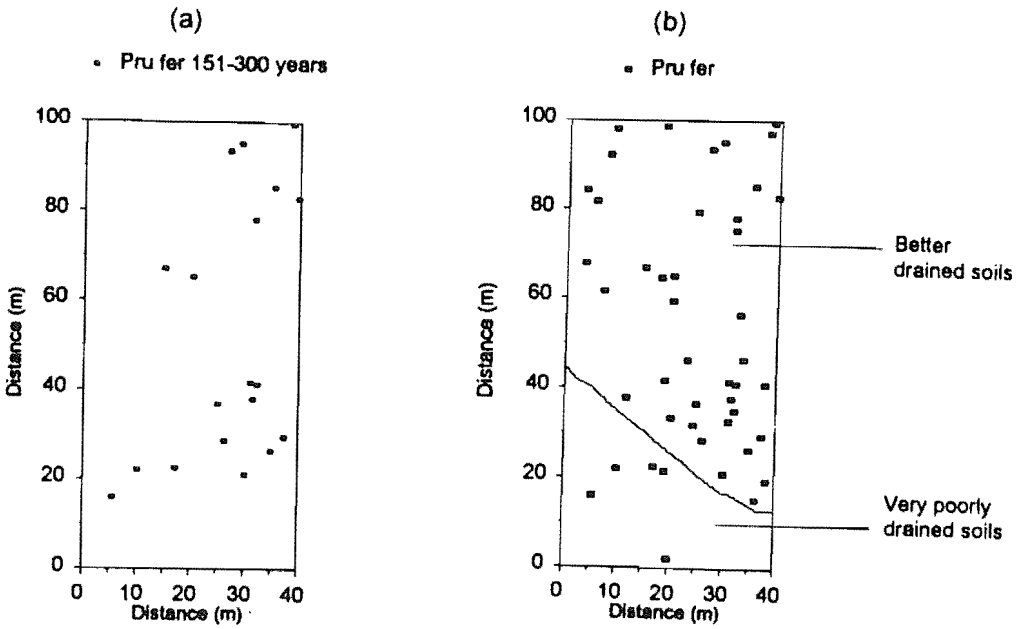
openings. *Prumnopitys* trees (151-300 years) were clumped at similar scales to *Prumnopitys* in stand S2 suggesting establishment in response to disturbances of similar size. In addition, the majority of *Prumnopitys* trees had established away from the area of poorly drained soils (Figure 6.9) suggesting a preference for better drained sites. *Dacrydium* was randomly dispersed in relation to other species (Table 6.12).

Small *Weinmannia* were clumped at small and large scales, having established away from large *Weinmannia* (Table 6.12), which suggests they were unable to regenerate beneath their own canopy. Large *Weinmannia* were also clumped, but at larger scales than in stand S1 which could reflect establishment in larger canopy openings. The lack of small scale clumping may reflect density dependant thinning and establishment in randomly dispersed canopy gaps. *Quintinia* (5-14cm dbh) established away from areas occupied by smaller *Weinmannia* and were clumped at small scales (Figure 6.9). This could reflect a preference for different establishment sites.

Table 6.11: Patterns of spatial dispersion for trees (by species age-class and size-class) in stand S3. Letters indicate significant ($P < 0.05$) deviation from a random distribution based on values of the function L *(t)*; C denotes a clumped distribution, . denotes a random distribution. Only size-classes with > 10 individuals were analysed.

		Diameter class (m)
	Species	1 . . . 5 . . . . 10 . . . . 15 20
Age-class (years)	*Dacrydium cupressinum* 151-300	. . . . C C C C C C C . . . .
	Dacrydium cupressinum 301-450	. C C C C C C C C C C C C C C C C C C C C
	Prumnopitys ferruginea 151-300	. . . . . C . . C C . C C C C C C
	Prumnopitys ferruginea 301-450	. . . . .
Size-class (cm)	*Weinmannia racemosa* 5-14	. C C C C C C C C C C C C C C C C C C C C
	Weinmannia racemosa ≥15	. . . . . C C . . . C C C
	Quintinia acutifolia 5-14	C . . . . .

Figure 6.9: (a) Stem map showing the clumped distribution of *Prumnopitys ferruginea* (151-300 years), (b) stem map showing the distribution of all *Prumnopitys ferruginea* stems (≥15cm dbh) and the distribution of differently drained soils, and (c) stem map showing the associations between *Weinmannia racemosa* ≥ 15cm dbh, *Weinmannia racemosa* 5-14cm dbh, and *Quintinia acutifolia* 5-14cm dbh in stand S3.



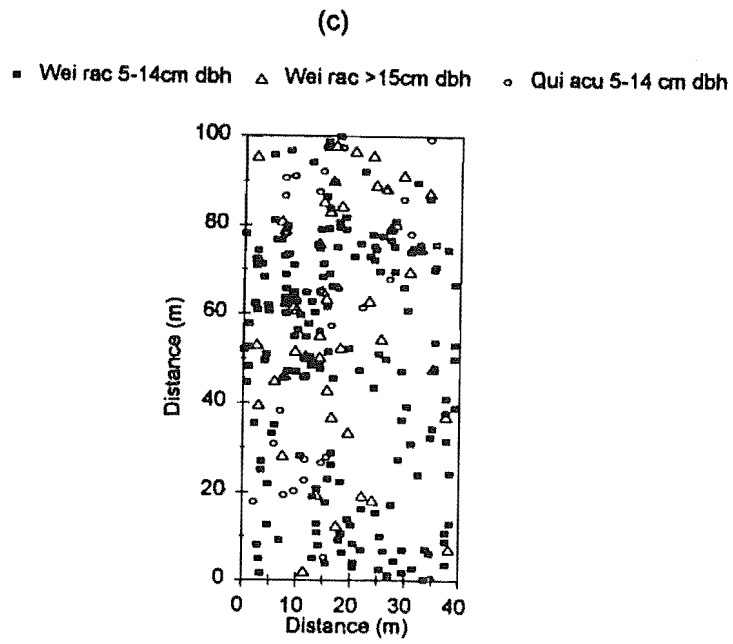


Table 6.12: Patterns of association for trees in stand S3 (by species, size and age-class) from the function $L_{12}(t)$. N & P denote significant ($P < 0.05$) negative and positive association at distances of t up to 20m, R denotes no significant association. Only size-classes with > 10 individuals were analysed.

		Age-class (years)			Size-class (cm)		
		DC 151-300	PF 301-450	PF 151-300	WR ≥ 15	WR 5-14	QA 5-14
Age-class (years)	Species						
	Dacrydium cupressinum 301-450	R	R	R	R	R	R
	Dacrydium cupressinum 151-300		R	R	R	R	R
	Prumnopitys ferruginea 301-450			R	R	R	R
	Prumnopitys ferruginea 301-450				N	N	N
Size-class (cm)	Weinmannia racemosa, ≥15					N	P
	Weinmannia racemosa, 5-14						N

6.3.9 Spatial structure

Alternating significant positive and negative values indicated patchiness in the spatial distribution of tree ages. Significant positive autocorrelation at small and large distances reflected the association of trees of similar ages within patches. Significant negative autocorrelation at intermediate distances corresponded to the distances between patches of different ages. The general shapes of the correlogram indicated that the three stands possessed different spatial structures. Stand S1 possessed the largest scale structure while the correlograms for *Dacrydium* in stands S2 and S3 indicated the presence of smaller patches of trees.

Stand S1

The distribution of *Dacrydium cupressinum* and *Lagarostrobos colensoi* tree ages in stand S1 had a significant spatial structure (Figure 6.10). The correlograms of tree age were globally significant at the α=0.05 level. For *Dacrydium* the shape of the correlogram indicated the presence of a large scale patch structure. Significant positive autocorrelation from distance class 1 to 11 (3-33m)

indicated the association of similar aged trees within a patch. Positive autocorrelation at small scales, distance class 1 (3m) indicated the presence of similarly aged adjacent trees within the larger patch structure. Significant negative association was present from distance classes 14-32 (42-96m) suggesting a continuous change in tree ages with increasing distance. The correlogram for *Lagarostrobos* indicated a similar trend to the correlogram for *Dacrydium*, however because the negative autocorrelation was not continuous it suggests that patches of differently aged trees are present rather than a continuous change in tree age. Significant negative autocorrelation was present between distance classes 19 (57m) and 29 (87m). Significant positive autocorrelation was present at various points between distance classes 1 (3m) and 12 (36m).

Stand S2

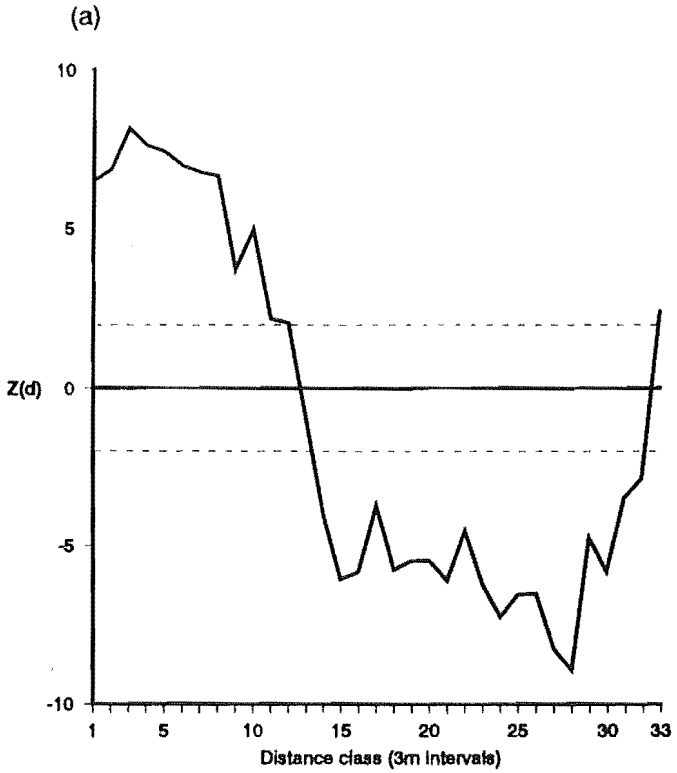
The distribution of *Dacrydium cupressinum* tree ages in stand S2 had a significant spatial structure. The correlogram of tree ages was globally significant at the α=0.05 level (Figure 6.11) The general shape of the correlogram suggests patches of even-aged trees were present. This was indicated by positive autocorrelation at distance classes 5 (15-m) and 19 to 20 (57-63m). This indicated a distance of 39m to 48m between patches of similarly aged trees. Significant negative association was present at distance classes 9 (27m) and 26 (78m) and represents distances between patches of dissimilar age.

The distribution of *Prumnopitys ferruginea* tree ages and *Phyllocladus alpinus* did not possess a significant spatial structure at the global significance level of α = 0.05.

Stand S3

The distribution of *Dacrydium cupressinum* tree ages had a significant spatial structure. The correlogram was significant at the α=0.05 level (Figure 6.12). Significant positive autocorrelation was present at distance class 1 (3m). This reflected the occurrence of small patches of adjacent trees of similar age. Significant negative autocorrelation was present at distance class 9 (27m) and

Figure 6.10: Spatial corellogram for (a) *Dacrydium cupressinum* and (b) *Lagarostrobos colensoi* in stand S1. Dotted lines indicate the 0.05 significance level.



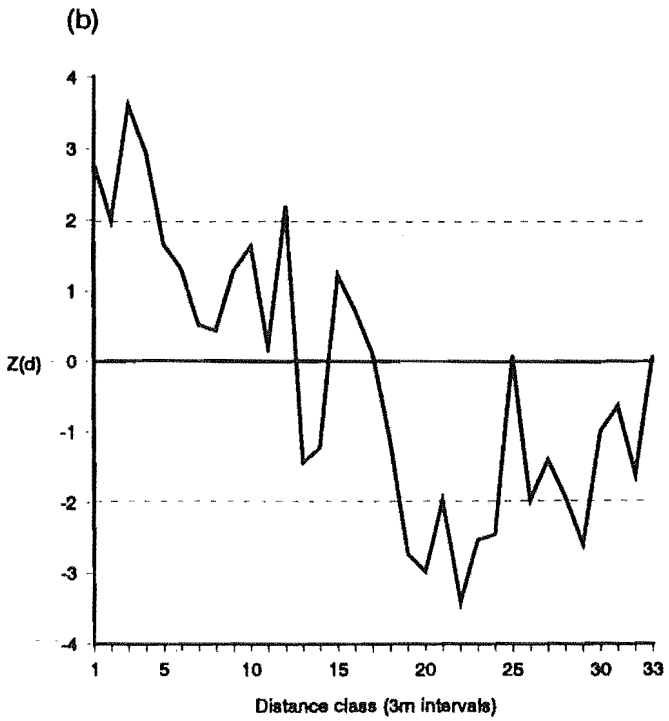


Figure 6.11: Spatial corellogram for Dacrydium cupressinum in stand S2. Dotted lines indicate the 0.05 significance level.

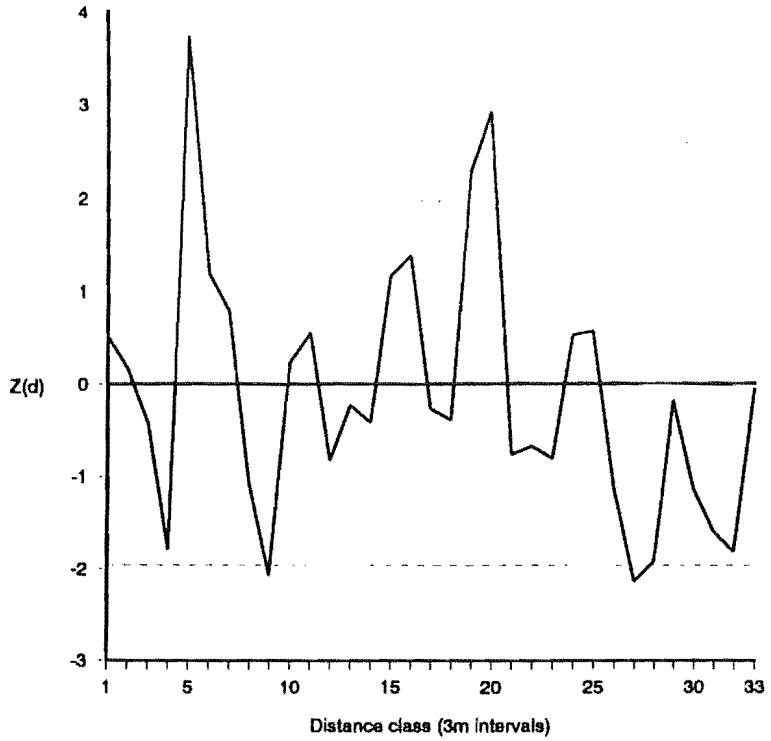
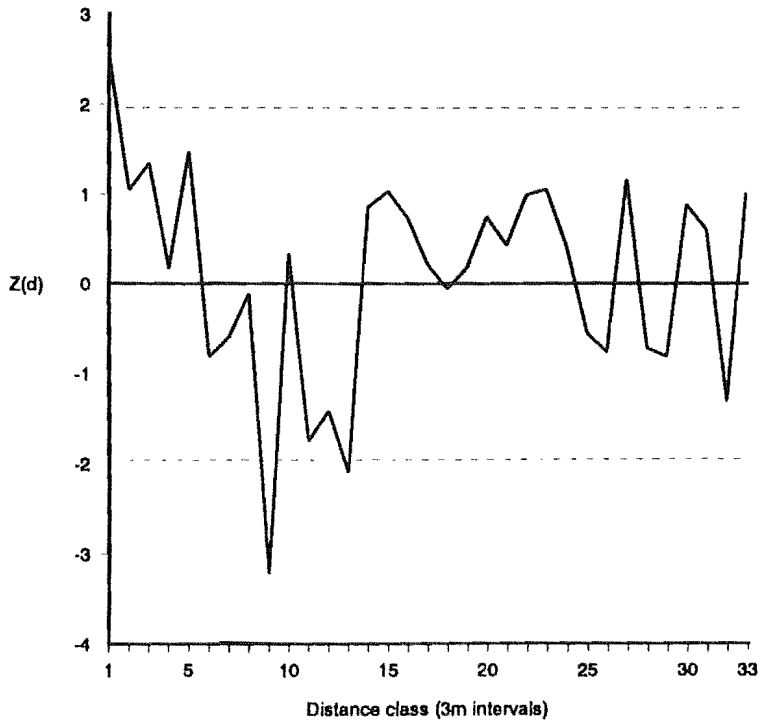


Figure 6.12: Spatial corellogram for Dacrydium cupressinum in stand S3. Dotted lines indicate the 0.05 significance level.



distance class 13 (39m) and represents distances between patches of dissimilar age. The distribution of tree ages of *Prumnopitys ferruginea* did not indicate a significant spatial structure at the α= 0.05 level.

6.3.10 Age-group identification and disturbance history

The age-groups identified from the agglomerative hierarchical clustering indicated differences in size, spatial and temporal discreteness. Stand S1 had the largest patch structure while stands S2 and S3 indicated more numerous, variable sized and variable aged patches.

Stand S1

The ordination scatter plot for *Dacrydium cupressinum* (Figure 6.13) did not indicate any specific patches so agglomerative hierarchical clustering was performed. From the dendrogram four groups were identified. Although the groups were spatially discrete their age ranges overlapped considerably (Table 6.13), for that reason these groups were not considered to be discrete even-aged patches initiated by separate temporally discrete disturbance events. The stem map suggests that the patch structure may be larger than the plot reflecting catastrophic disturbance. The plot of distance along stand (0-100m) against tree age for *Dacrydium* (Figure 6.13) reflected the pattern of establishment, with groups 2 and 3 suggesting synchronous establishment, however the distribution of group 4 suggests a period of more temporally protracted establishment. The protracted and overlapping age distribution of the groups suggests establishment of *Dacrydium* occurred over a prolonged period. This is consistent with the broad age range of the regenerating stand S1r. The temporal and spatial distribution of tree ages appeared consistent with the type of spatial structure suggested by the correlogram.

For *Lagarostrobos* the ordination scatter plot indicated two main groups that were relatively discrete, however agglomerative hierarchical clustering further subdivided these into four groups that were spatially discrete (Figure 6.14). The groups had narrower age ranges than for *Dacrydium* (Table

Figure 6.13: (a) Scatter diagram for *Dacrydium cupressinum* obtained from the ordination of the association measures reflecting tree age difference and spatial proximity, (b) stem map of age groups identified from cluster analysis for *Dacrydium cupressinum*, and (c) the distribution of *Dacrydium cupressinum* tree ages along the stand with groups 1-4 identified from cluster analysis superimposed for stand S1.

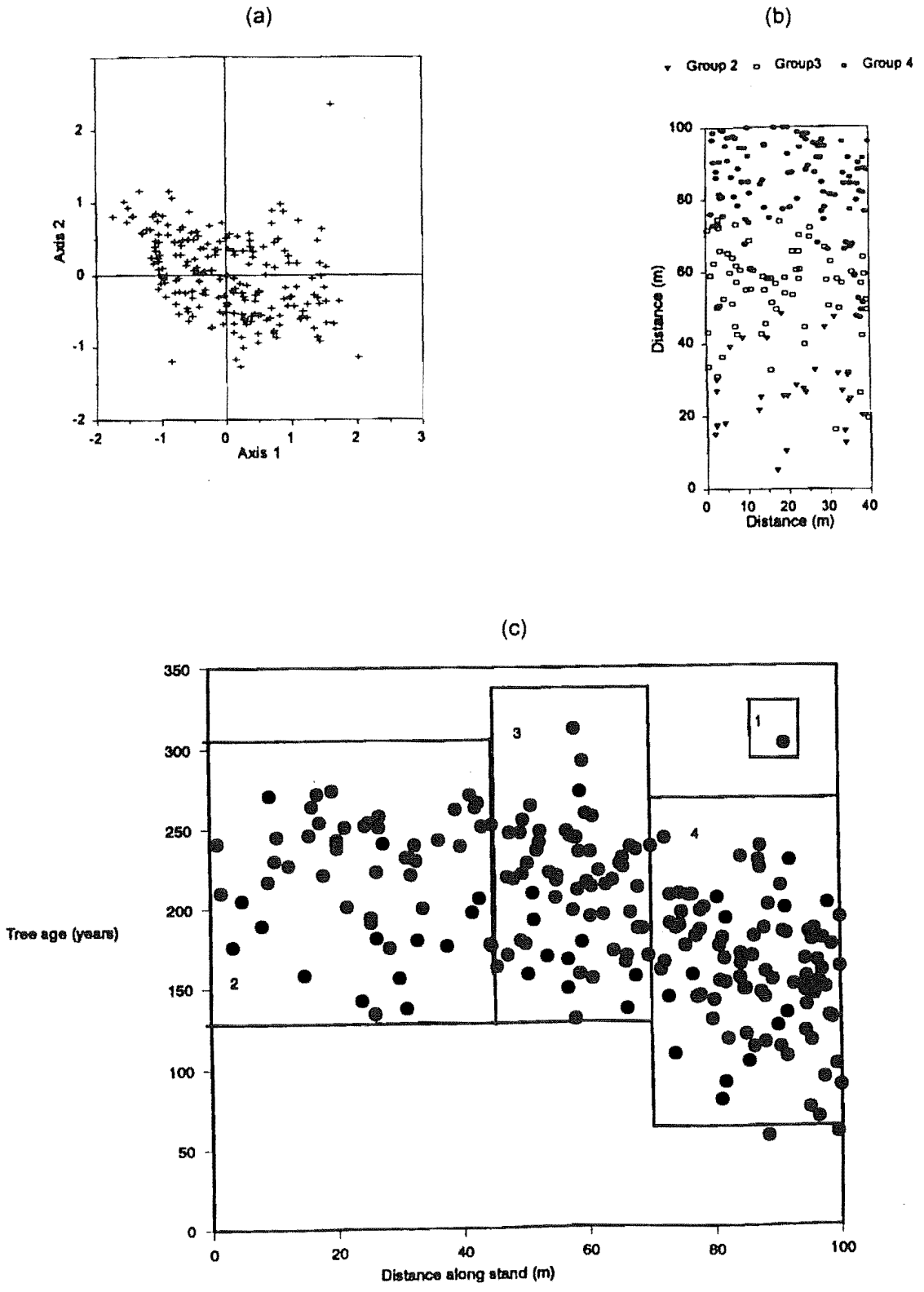
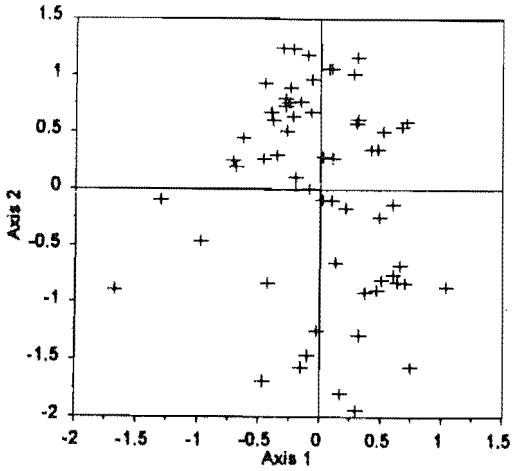
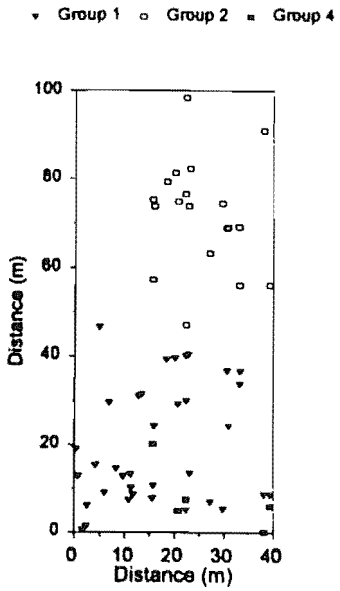


Figure 6.14: (a) Scatter diagram for *Lagarostrobos colensoi* obtained from the ordination of the association measures reflecting tree age difference and spatial proximity, (b) stem map of age groups identified from cluster analysis for *Lagarostrobos colensoi*, and (c), age class frequency distributions for groups 1 and 2 for stand S1 Age classes are 25 year intervals beginning at 126-150 years.

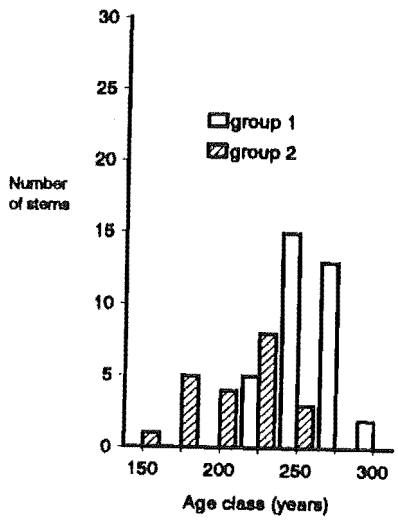
(a)



(b)



(c)



6.13), suggesting that *Lagarostrobos* may be more limited in its establishment period. The two main groups (groups 1 & 2) had mean ages of 246 years and 194 years (Table 6.13) with overlapping unimodal age-class frequency distributions (Figure 6.14) showing that initial establishment of group 1 occurred before group 2.

Table 6.13: Mean age (± SD) and age range of groups derived from agglomerative hierarchical clustering for *Dacrydium cupressinum* and *Lagarostrobos colensoi* in stand S1.

Dacrydium cupressinum	n	Mean	S.D.	Min	Max	Range
1	1	312				
2	32	227	37	137	274	137
3	71	207	40	108	312	204
4	115	169	46	56	302	246
Lagarostrobos colensoi						
1	36	246	18	216	276	60
2	21	194	30	132	240	108
3	1	111				
4	4	194	24	162	208	46

Stand S2

The ordination diagram of the two dimensional matrix of association values indicated the presence of overlapping patches (Figure 6.15). Agglomerative hierarchical clustering identified 10 patches. However, group 8 was split into two, (groups 8 and 11) because the stem map indicated the presence of two separate relatively discrete groups which had different ages.

The groups identified indicated the presence of a complex range of overlapping patches of *Dacrydium* trees. These varied in size (2 to 21 individual trees), and spatial and temporal discreteness (Table 6.14; Figure 6.15) Groups 2,3,5,6,7,9, and 10 were relatively even-aged. Groups 1, 4, and 8, had wider age ranges. Most patches occurred in relatively discrete regions of the plot, although there was

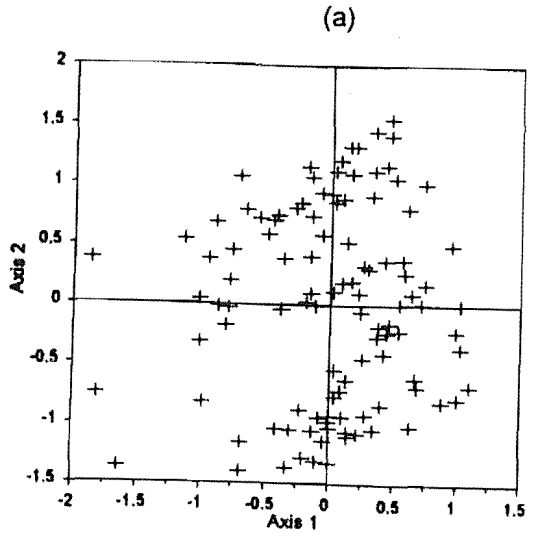
some spatial overlap between young and old patches, e.g., Groups 1 and 2, and groups 1 and 3. An exception was group 5 which suggested more sporadic regeneration of single *Dacrydium* stems. Groups 9 and 10 possessed the oldest trees representing trees from remnant cohorts with group 9 indicating the upper age limit of *Dacrydium* trees for this stand. From a stem map of the tree ages it was evident that within the large patches smaller scale patches consisting of 2 or 3 similarly aged adjacent trees occurred. This scale of patchiness was not indicated by the correlogram.

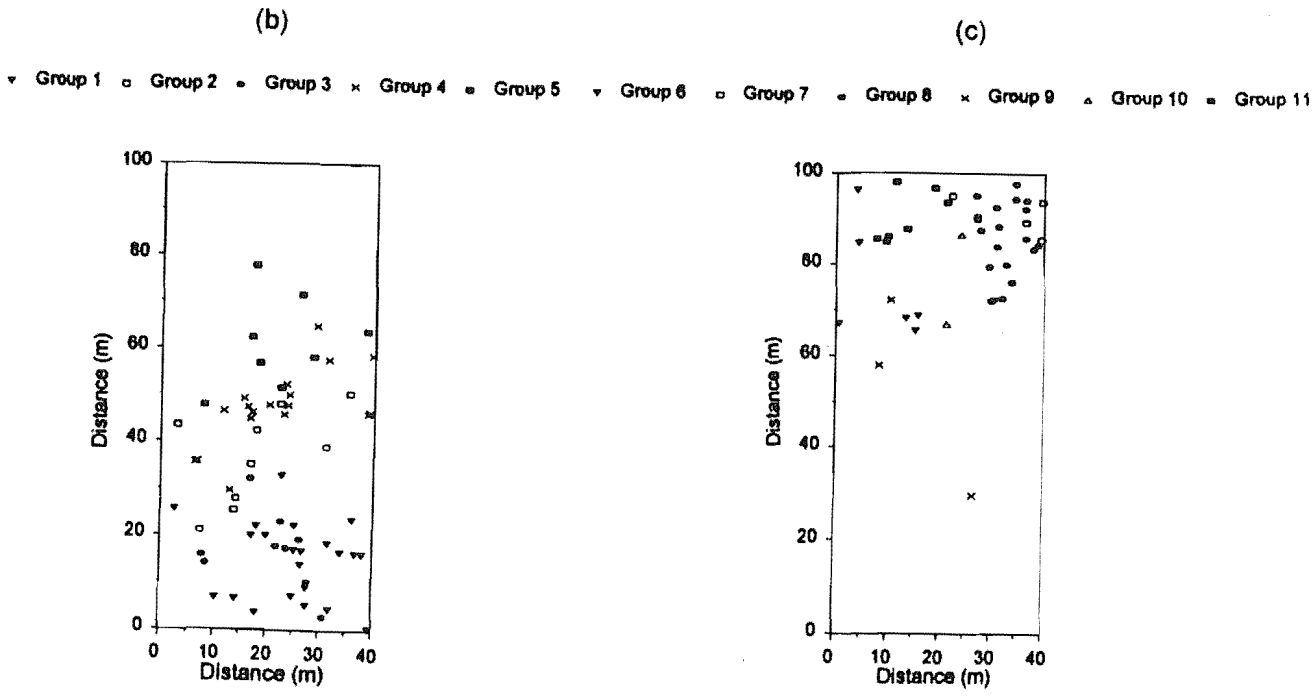
The age range and the spatial arrangement of the above groups indicated a regeneration pattern where sporadic gap phase recruitment of *Dacrydium cupressinum* has occurred on a scale from one to several trees.

Table 6.14: Mean age (± SD) and age range of groups derived from agglomerative hierarchical clustering for *Dacrydium cupressinum* in stand S2.

Group	n	Mean	S.D.	Min	Max	Range
1	21	155	54	73	252	179
2	9	359	31	359	461	102
3	8	306	23	280	356	76
4	18	211	45	145	318	173
5	8	90	27	47	127	80
6	6	193	19	167	225	58
7	4	132	36	84	177	93
8	19	301	39	227	373	146
9	3	682	18	660	705	45
10	2	507	3	504	510	6
11	7	361	39	307	429	122

Figure 6.15: (a) Scatter diagram for *Dacrydium cupressinum* obtained from the ordination of the association measures reflecting tree age difference and spatial proximity, (b) stem map of age groups identified from cluster analysis for *Dacrydium cupressinum* in stand S2.





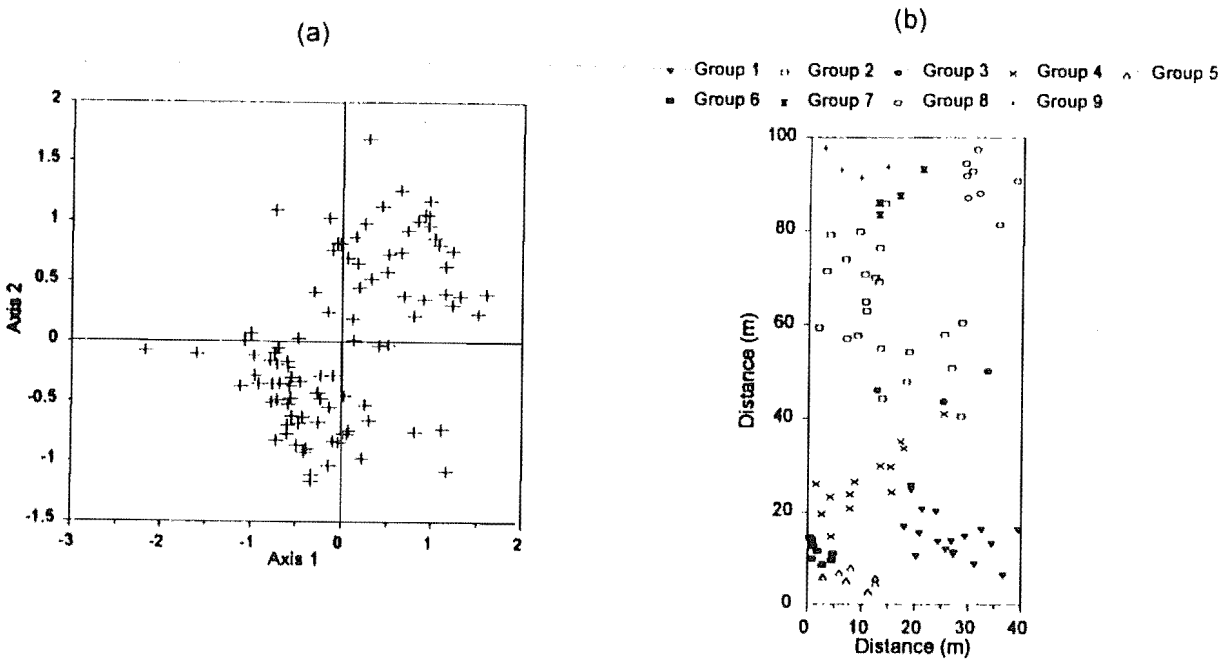
Stand S3

The ordination diagram of the two dimensional matrix of association values indicated two main groups (Figure 6.16), but these did not represent spatially or temporally discrete groups of trees. Nine groups were identified from agglomerative hierarchical clustering (Table 6.15). Most groups occupied discrete regions of the plot with the exception of the older group 3 which overlapped with the younger group 2 (Figure 6.16). The mean ages of spatially discrete groups were similar for groups 2, 6, 8 and 9 and groups 1, 4 and 5. The presence of disjunct spatially discrete groups of similar mean age indicated a disturbance history where a period of protracted gap formation had occurred. This resulted in groups such as 6 and 8, which established at similar times but in different areas of the plot. Groups ranged in size from 3 to 22 individuals.

Table 6.15: Mean age (± SD) and age range derived from agglomerative hierarchical clustering for *Dacrydium cupressinum* in stand S3.

Group	n	Mean	S.D.	Min	Max	Range
1	17	388	47	196	368	172
2	22	293	58	217	396	179
3	3	562	46	522	627	105
4	13	410	54	274	489	215
5	7	379	44	302	452	150
6	8	297	45	208	354	146
7	4	452	26	425	481	56
8	8	313	43	238	389	151
9	4	318	37	259	362	103

Figure 6.16: (a) Scatter diagram for *Dacrydium cupressinum* obtained from the ordination of the association measures reflecting tree age difference and spatial proximity, (b) stem map of age groups identified from cluster analysis for *Dacrydium cupressinum* in stand S3.



6.3.11 Treefall characteristics and gap regeneration characteristics

Different patterns of treefall/canopy tree death and gap regeneration characteristics were evident between the two terraces sampled. Gaps on terrace 1 were not sampled because of logging effects.

***Treefall characteristics*:**

Terrace 2

For the nineteen gaps measured, standing dead and snapped *Dacrydium* were the most frequent canopy gap makers (Table 6.16). However, dead stems of *Quintinia* and unidentified angiosperms (most likely *Quintinia acutifolia*) were frequently encountered. These stems generally contributed to existing gaps caused by large *Dacrydium*. The number of treefalls and standing dead trees in a gap ranged from 1 to 7 trees, with 63% of the gaps formed by more than one tree.

Terrace 3

Canopy gaps were most frequently formed by large (59 ±9.3cm dbh) *Dacrydium* trees which were commonly snapped in contrast to *Lagarostrobos* which were usually found dead standing (Table 6.17). Unidentified angiosperms (most likely *Weinmannia racemosa* since the population structure of stand S3 indicated the presence of few large *Quintinia* stems) were most commonly found in gaps. These were most commonly uprooted or found dead standing. Gaps were formed by 1-6 trees with a mean of 3.

Table 6.16: Treefall characteristics, terrace 2.

	Frequency				
Species	Uproot	Snap	Standing Dead	Mean dbh ± S.D.(cm)	dbh Range (cm)
Dacrydium cupressinum	2	5	7	53.0±13	30-64
Lagarostrobos colensoi	0	0	2	33.5±4	30-37
Prumnopitys ferruginea	6	0	0	25.3±3	20-26
Quintinia acutifolia	12	2	0	24.0±2	21-30
Weinmannia racemosa	0	0	0		
Unidentified angiosperms	14	5	1	25.7±3	22-30

Table 6.17: Treefall characteristics, terrace 3.

	Frequency				
Species	Uproot	Snap	Standing Dead	Mean dbh ±S.D. (cm)	dbh Range (cm)
Dacrydium cupressinum	1	6	1	59.0±9	45-80
Lagarostrobos colensoi	2	0	6	38.0±9	29-52
Prumnopitys ferruginea	2	3	3	40.0±8	31-51
Quintinia acutifolia	0	0	1	27.0	0
Weinmannia racemosa	0	0	1	24.0	0
Unidentified angiosperms	8	3	9	28.0±5	20-40

Gap and Regeneration characteristics:

The gap regeneration characteristics, suggested that *Weinmannia* and *Quintinia* had an ability to regenerate in smaller scale canopy gaps than the conifers, with *Quintinia* dominating gaps on terrace 2 and *Weinmannia* dominating gaps on terrace 3 (Table 24).

Terrace 2

Canopy gaps ranged from 32 to 256m^2 and expanded gaps from 98 to 369m^2. The mean d/h ratio of 0.3 reflected the relatively small size of the gaps (Table 6.18). Numbers of seedling and saplings of *Dacrydium*, *Lagarostrobos* and *Prumnopitys* were variable in relation to expanded gap size. However the highest number of *Dacrydium* seedlings and saplings were present in the largest gap (256m^2, d/h = 0.6). Although *Lagarostrobos* seedlings and saplings within gaps were the most abundant of the conifer species enumerated, this was not reflected by the number of stems present in the gaps.

Gaps were dominated by *Quintinia* (290ha^{-1}) and *Weinmannia* (208ha^{-1}), however *Weinmannia* stems were generally small with a mean dbh of 9 ± 3cm dbh compared to 18 ± 4cm dbh for *Quintinia*. Many *Phyllocladus* were also present, however, stems were mainly confined to four of the gaps with a maximum number of 774 stems ha^{-1}. Stem numbers were variable in relation to gap size apart from *Weinmannia*, which was related to expanded gap size (r^2=0.52). However, the largest number of stems of *Phyllocladus* occurred in the largest gap.

Terrace 3

Canopy gaps ranged from 38 to 162m^2, while expanded gaps ranged from 82 to 309m^2. Relatively few conifer seedlings were present, of which seedlings and saplings of *Prumnopitys* were most common (Table 24).

Gaps were generally dominated by stems of *Weinmannia* and *Quintinia*, of which stems of *Weinmannia* (mean dbh of 12.0± 2.1cm) were c. six times more abundant than stems of *Quintinia* (mean dbh of 10.5± 9.0cm). Stems of *Lagarostrobos* and *Phyllocladus* were rare, and stems of *Dacrydium* occurred in low numbers. However at the end of the second transect one large gap was encountered c. 0.8ha in size. Here the forest was heavily disturbed, consisting of sparse large canopy trees > 40cm dbh (60 stems ha^{-1}) with frequent treefalls > 40cm dbh (50 stems ha^{-1}). The regeneration characteristics were determined from a sapling count and from the size-class frequency distribution of conifer stems in a 40m×40m plot. The number of saplings and the distribution of stems in different size-classes (Figure 6.16) indicated abundant regeneration of *Dacrydium* (631 saplings ha^{-1}) and *Lagarostrobos* (613 saplings ha^{-1}) with more moderate regeneration of *Prumnopitys ferruginea* (250 saplings ha^{-1}) (Figure 6.17)

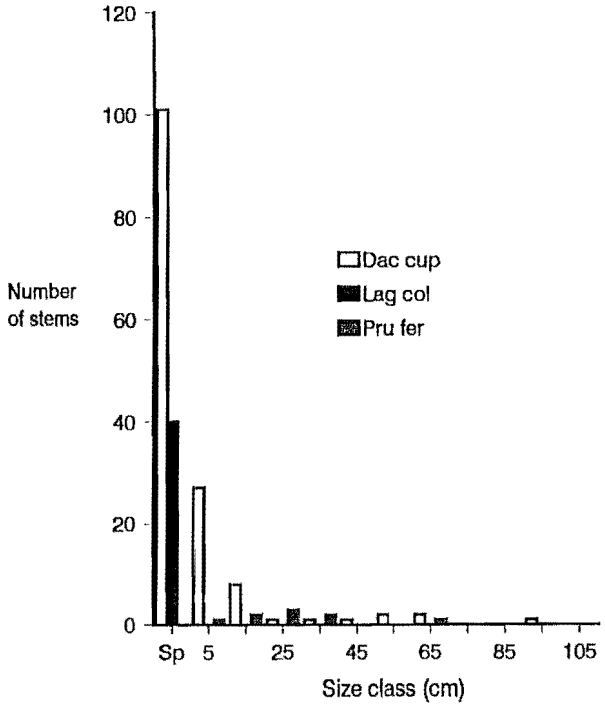
Table 6.18: Gap characteristics and regeneration characteristics for terrace 2 & 3. (d/h = gap diameter/canopy height)

	Terrace 2		Terrace 3	
Gap characteristics				
Median canopy gap size (m^2)	99		97	
(range)	32-256		38-162	
Median expanded gap size (m^2)	171		214	
(range)	98-396		82-309	
Mean canopy/expanded gap ratio	0.5		0.4	
(range)	0.2-0.7		0.3-0.6	
Mean d/h ratio	0.3		0.5	
(range)	0.2-0.7		0.3-0.6	
Gap Regeneration characteristics				
Mean density of seedlings & saplings ha^{-1}	Seedlings ha^{-1}	Saplings ha^{-1}	Seedlings ha^{-1}	Saplings ha^{-1}
Dacrydium cupressinum	54	192	18	48
Lagarostrobos colensoi	123	135	66	30
Prumnopitys ferruginea	116	83	111	68
Mean density of trees ha^{-1} (≥5cm dbh)				
Dacrydium cupressinum	117		56	
Lagarostrobos colensoi	16		18	
Prumnopitys ferruginea	18		58	
Phyllocladus alpinus	157		19	
Weinmannia racemosa	208		645	
Quintinia acutifolia	290		110	

6.3.12 Soil drainage for the 40m×40m plots

The dense *Lagarostrobos* dominated stands 1.7 and 3.2 occurred on poorly drained soils as indicated by their mean aerobic depth of 2.8±2.7cm and 3.9±3.4cm respectively. By contrast stand 1.4 dominated by large stems of *Dacrydium* had considerably better drainage as indicated by a mean aerobic depth of 10.2± 2.1cm.

Figure 6.17: Size-class frequency distribution for the large gap on terrace 3. Sp = saplings, size classes are 10cm intervals beginning at 5-14cm dbh.



6.3.13 Soil profile classes and soil drainage for stands S1, S2 & S3

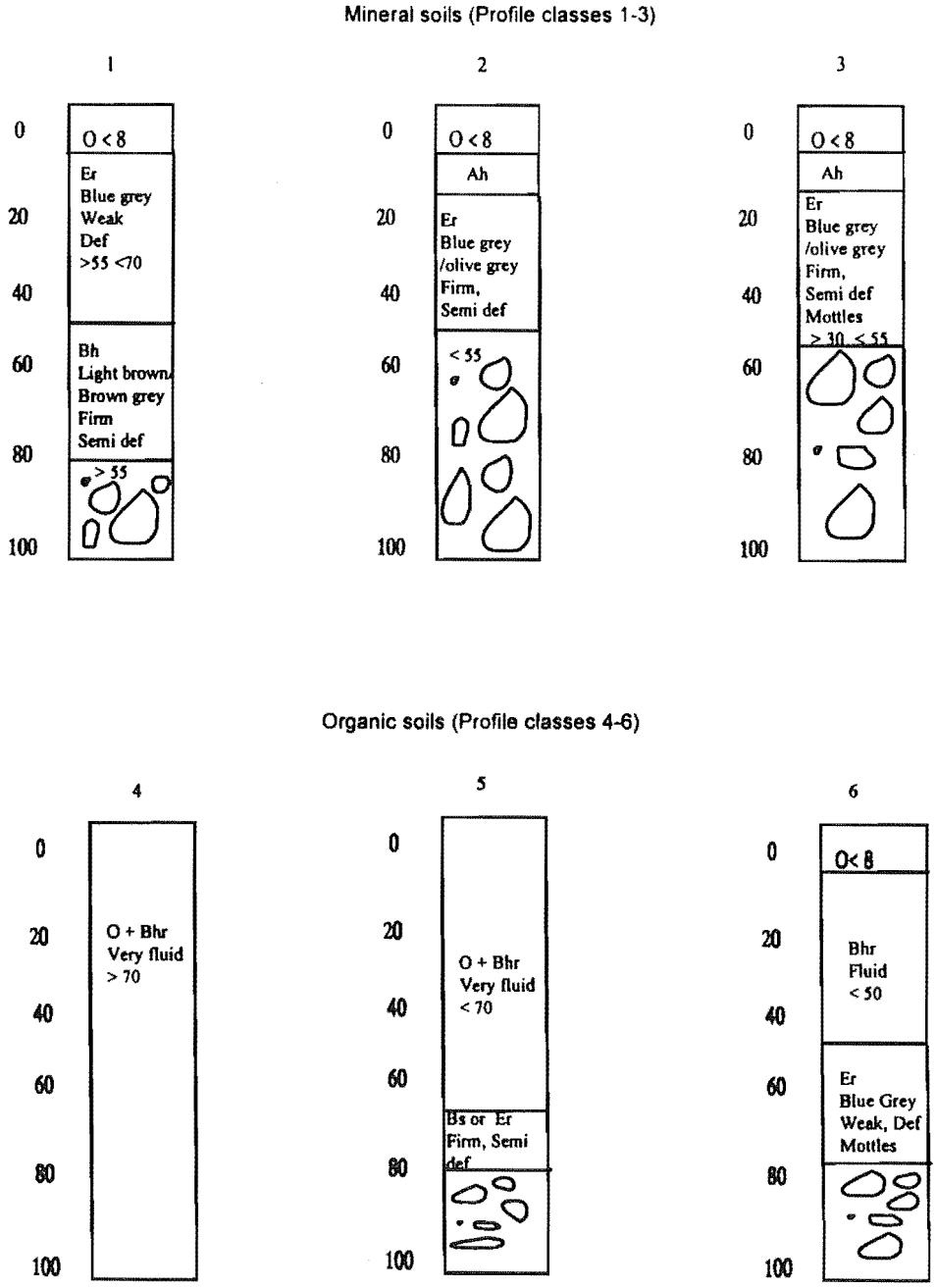
From the 156 soil descriptions soils were grouped into six different profile classes (Figure 6.18). The profile classes were split between mineral and organic soils. The three stands had different frequencies of mineral and organic soils. The soils varied from deep organic soils (fluid mucks) which had little or no horizon differentiation to soils possessing distinctly eluviated horizons (Er) formed in the mineral fines (loess deposits) indicating a strong leaching environment. The eluviated horizons were commonly bright blue grey in colour, and firm to soft in consistency and frequently overlain by more fluid horizons. Structural roots were evident throughout the fluid horizons but did not penetrate the eluviated horizons. In addition some soils possessed mottling, mainly in the shallower soils of stand S3 indicating a more aerobic rooting environment which could reflect fluctuation in the level of the water table. The soils can generally be classified as fluid mucks (81 soils) and gley podzols (75 soils) all of which had a silty loam texture.

The soils increased in depth from stand S3 on the youngest terrace to stand S1 on the oldest terrace, which also had the most poorly drained soils (Table 6.19). On terrace 1 loess deposits were deepest, 80-100cm (pers comm P.Almond), and here were frequently found to be overlain by a metre of fluid organic material. The deep soils in stand S1 were consistently very poorly drained and the fluid muck horizons (O+Bhr, class 4+5) were frequently so fluid that the soil would flow off the auger.

In stand S2 five different classes of soil were recognised most of which were organic soils ranging from fluid mucks similar to those in stand S1 to more shallow soils (classes 2, 3, & 6) which possessed strongly eluviated horizons underlain by gravels. However, the deep organic soils were much better drained than those in stand S1 which may indicate improved run off. The mineral soils were better drained than the organic soils.

Soils in stand S3 on the youngest terrace, in contrast to the deep soils of stand S1 were predominantly shallow and had substantially less loess deposits, attributed to the younger age of the

Figure 6.18: Classification of the soil profiles sampled in the three stands S1, S2 & S3. Descriptions refer to the horizon name, colour, strength, fluidity and horizon depth limits (cm).



terrace. Here all six profile classes were recognised, half of which were mineral soils. The shallow mineral soils (classes 2 & 3) were underlain by gravels and ten of these (class 3) had distinct mottles reflecting a fluctuating water table resulting in an improved rooting environment, as indicated by an aerobic depth of 10.8±6.3cm. The shallow mineral soils, profile classes 2 and 3 were better drained than the deep organic soils of profile classes 4 and 6.

Table 6.19: The frequency (#) of different soil profile classes and the mean aerobic depth (cm) for each profile class within stands S1, S2 and S3.

	Stand S1			Stand S2			Stand S3		
Profile class	#	Aerobic depth ± S.D.(cm)	Soil depth (cm)	#	Aerobic depth ± S.D.(cm)	Soil depth (cm)	#	Aerobic depth ± S.D.(cm)	Soil depth (cm)
1	1	0	>100	0			1	14	
2	0			4	16.3±4.8	55±5	19	7.8±4.5	49±8
3	0			1	12	40	10	10.8±6.3	50±10
4	35	1.2±1.6	>100	34	10±6.0	96±10.2	10	1.9±2.0	89±12
5	16	1.1±1.3	>100	5	8.2±3.5	92±16	2	17.5±6.5	90±10
6	0			9	6.6±3.9	50±17	10	6.1±2.5	62±14
	Stand mean	1.2±1.5	>100		9.7±5.7	80±20		7.7±5.7	62±19

6.4 Discussion

6.4.1 Introduction

The results showed that stand composition and structure were significantly different between the dominant stand on each of the three differently aged glacial terraces. This forest variation reflected environmental variation related to changes in soil drainage/stage of soil development, and differences in disturbance history associated with these changes. In this chapter the separate and combined influence of environment and disturbance on forest variation are discussed.

6.4.2 Terrace forest variation

Stand structure, disturbance histories and regeneration patterns

In the dense conifer dominated lowland forests of south Westland studies have described differences in stand structure that reflect spatial and temporal variation of disturbance histories (Cornere 1992, Duncan 1993). In these forests natural disturbances create different sized canopy openings that occur at different frequencies, caused by factors such as flooding and windthrow (Poole 1937; Six Dijkstra et al.1985; Cornere 1992; Duncan 1993), and synchronous canopy collapse reflecting stand age (Six Dijkstra et al. 1985; Lusk & Ogden 1992; Ogden & Stewart 1995). Such natural disturbances are considered critical for successful regeneration of the dominant trees in these lowland forests (Ogden & Stewart 1995).

Disturbance histories commonly vary between forest types, e.g., in *Dacrycarpus dacrydiodes* dominated forest on recent alluvial surfaces flooding is common (Duncan 1993), while in terrace rimu (*Dacrydium cupressinum*) forest disturbance is attributed to windthrow (Hutchinson 1932; Poole 1937; Six Dijkstra *et al.* 1985; Cornere 1992). In the North Island cyclones and volcanic activity have affected large areas of forest (Shaw 1983; McKelvey 1963). In montane *Libocedrus bidwillii* forest mass movement induced by torrential rain and tectonic activity affects large areas of forest on the steeper terrain (Clayton-Greene 1977; Stewart & Rose 1989). Outside New Zealand other disturbance types are important, e.g., in Tasmania fires are important for the regeneration of

Athrotaxis selaginoides and *Phyllocladus asplenifolius* (Read & Hill 1988) and for *Austrocedrus chilensis* in Patagonia (Veblen et al. 1992), while tropical cyclones have resulted in dense stands of *Agathis macrophylla* in the Solomon Islands (Whitmore 1966). These different types of disturbance can also differ in the scale of canopy opening they create e.g., flooding generally affects relatively large tracts of forest, while wind creates a continuum of gap sizes from large scale blowdowns to single tree falls. In the present study temporal and spatial variation of disturbance histories occurred across the one forest type, which was reflected by differences in vertical structure, size and age-class frequency distributions and by differences in the spatial distribution of tree ages between stands S1, S2 and S3.

For stand S1 relatively even-aged recruitment of *Dacrydium* and *Lagarostrobos* suggested that catastrophic disturbance had occurred. The stand was the most uniform, being relatively even-aged with most stems of *Dacrydium* and *Lagarostrobos* confined to the upper strata. Although even-aged, establishment occurred over c.200 years for *Dacrydium* and c.150 years for *Lagarostrobos*. For *Dacrydium* this partly reflected protracted establishment as reflected by the age structure of the regenerating stand S1r, where establishment occurred over at least 100 years.

A stand may be regarded as even-aged if most of the individuals fall within 10% of the normal attainable age. Taking 700 years as such an age for *Dacrydium* trees in south Westland, a stand having an age range of 70 years can be classified as even-aged. For stand S1 the age-ranges of *Dacrydium* and *Lagarostrobos* fell outside this definition and are classified as relatively even-aged. This definition refers to situations in which a site is "fully stocked" with seedlings over a time period which is much less than the normal attainable age (Ogden 1985a).

For stand S2 *Dacrydium* age-groups were both even-aged and relatively even-aged suggesting a gap-phase mode of regeneration from recurrent, but smaller scale disturbances. This frequently disturbed stand was multi-tiered with *Dacrydium* trees distributed relatively evenly between the

different height classes. The number of trees in each group and their age range was generally less than those in stand S1, reflecting the creation of medium to small sized canopy openings where canopy closure by adjacent trees would prevent protracted establishment. The establishment response of *Phyllocladus* and *Prumnopitys* was not so clear because of the lack of spatial autocorrelation in the distribution of tree ages. Lack of pattern in the distribution of tree ages may simply reflect time since disturbance. With stand age the response to past disturbance will become less clear as trees succumb to the competitive effects of neighbours. However, it was evident from the age-class frequency distribution of *Prumnopitys* that sporadic establishment had occurred, with peak establishment of *Prumnopitys* coinciding with that of *Dacrydium*. Synchronous establishment of coexisting conifer species has also been described for other New Zealand forests (Lusk & Ogden 1992; Duncan 1993).

In stand S3, the discontinuous but broad unimodal age-class frequency distribution of *Dacrydium* and the distribution of spatially segregated, similarly aged groups of *Dacrydium* across the stand suggested that a progressive pattern of canopy mortality had occurred. This had resulted in a more uniform stand than stand S2. Progressive canopy mortality could reflect stand age predisposing trees to successive windstorms, rather than protracted establishment in response to a single massive disturbance. The greater age-range of the *Dacrydium* age-groups compared to stand S2 presumably reflects overlapping gap formation episodes. Progressive mortality of the overstorey appears to have occurred over 250-300 years with the peak in the age-class frequency distribution for *Dacrydium* in the sixteenth and seventeenth centuries presumably coinciding with the period of maximum canopy opening. Progressive canopy mortality of mature podocarps has been postulated for a North Island conifer dominated forest (Lusk & Ogden 1992), while others have attributed similar age-class frequency distributions to more synchronous canopy collapse (Six Dijkstra et al. 1985; Norton et al. 1988; Ogden & Stewart 1995). The occurrence of mature relatively even-aged groups of *Dacrydium* trees in lowland forests (Six Dijkstra *et al.* 1985; Cornere 1992, Lusk & Ogden 1992) would make progressive canopy collapse a realistic scenario.

Catastrophic and gap-phase patterns of regeneration showed by the conifers in this study have been widely documented for a variety of conifers in montane and lowland, temperate and tropical evergreen forests in the southern hemisphere (Whitmore 1966; Ogden 1985b; Ogden 1987; Cullen 1987; Read & Hill 1988; Duncan 1993). A common theme of these studies has been the ability of the less shade tolerant conifers to regenerate both after canopy gap formation and after catastrophic disturbance, e.g., *Libocedrus bidwillii* in the montane forests of New Zealand (Veblen & Stewart 1982; Stewart & Rose 1989), *Agathis australis* in the North Island of New Zealand (Ogden et al. 1987) and *Athrotaxis selaginoides* in Tasmania (Cullen 1987; Read & Hill 1988). This was also a feature of *Dacrydium cupressinum* in the present study.

The distinction between catastrophic and gap-phase patterns of regeneration is arbitrary. Veblen (1992) defines catastrophic regeneration as >10000m^2. However, massive establishment (as had occurred in stand S1) does not necessarily require an exogenous catastrophic disturbance, but can reflect relatively synchronous overstorey mortality (Stewart 1982). Gap-phase regeneration covers both intermediate down to the smallest scales, where regeneration occurs in single tree-fall gaps.

In addition to the major patterns of disturbance described above, stands were also subject to more minor disturbances as reflected by the treefall characteristics. Regeneration of *Weinmannia* and *Quintinia* were attributed to establishment in these smaller canopy openings created by one or two large treefalls. Small canopy openings are similarly important for the regeneration of angiosperms in Southern Cape forests (Geldenhuys & Maliepaard 1983). However, the population structure of *Weinmannia* in all three stands suggested a more continuous mode of regeneration. Frequent formation of small gaps or profuse suckering could account for such population characteristics. In other population studies on *Weinmannia* both gap phase and catastrophic regeneration patterns have been documented (Stewart 1986; Wardle 1991) with catastrophic regeneration confined to angiosperm dominated forest types. In stand S1 there was no evidence that *Weinmannia* had catastrophically regenerated, although catastrophic regeneration of *Dacrydium* and *Lagarostrobos*

had occurred.

The contrasting regeneration responses to the different disturbance histories suggest that *Dacrydium*, *Lagarostrobos*, and *Phyllocladus* may have a competitive advantage over *Weinmannia* and *Quintinia* in large to intermediate scale canopy openings.

Patterns of stand development for the different disturbance histories

Stand S1

Patterns of stand development post catastrophe have been described for different coniferous forests in the southern hemisphere (Veblen 1982; Cullen 1987; Ogden 1985a; Duncan 1993; Ogden & Stewart 1995), and are generally comparable to stand S1 where massive establishment of *Dacrydium* and *Lagarostrobos* appeared to have occurred. Stands resulting from catastrophes are relatively even-aged with relatively even-sized trees. Once established such stands are subject to a period of self thinning (Ogden 1985a).

Where conifers coexist with angiosperms (and in the absence of *Nothofagus* spp.) catastrophic disturbances generally promote the regeneration of dense stands of conifers relative to the angiosperms (Veblen 1982). However, little quantitative data has been provided to explain why conifers preferentially establish over angiosperms, even though this pattern of stand development has been recognised from some early studies (Womersley 1958). Studies have suggested that conifers favour regeneration in large gaps because of their less shade tolerant nature and their height growth response to increased light. However, when conifers are associated with *Nothofagus* species, they are poorly represented in stands that regenerate after a catastrophe, e.g., in Chile *Nothofagus* species preferentially regenerate following catastrophic disturbance due to the production of huge quantities of easily dispersed seed, in conjunction with an ability to grow rapidly on open sites (Veblen 1982). This contrasts to the regeneration strategy of *Dacrydium* as its seed production shows a high degree of periodicity and is reliant upon birds for dispersal (Norton & Kelly 1988), and New Zealand

conifers in general have growth rates between 44% and 51% that of associated angiosperms (Lusk & Ogden 1995).

For stand S1 there was no evidence to suggest that either *Weinmannia* or *Quintinia* had established massively, although the association of larger stems of both species with *Lagarostrobos* stems (151-251) years could reflect synchronous establishment as large diameter *Weinmannia* have been aged at 250 years and *Quintinia* at 250-300 years in north Westland (June 1982). Alternatively, this could simply reflect preferential establishment or growth to maturity beneath the more diffuse canopy of *Lagarostrobos* (per obs) where subcanopy light levels are likely to be higher relative to the more dense *Dacrydium* canopy.

Although *Dacrydium* and *Lagarostrobos* established at similar times in stand S1 they were spatially segregated. Reasons for this were unclear, but could be related to environmental heterogeneity at the time of establishment, the presence of established seedlings prior to disturbance of one of the species and differences in height growth response to increased light. The rapid growth of *Lagarostrobos* seedlings in well lit environments (Chapter 3) may confer a competitive advantage.

The intensity of catastrophic disturbance can also effect patterns of stand development (including stand composition). Less intense catastrophes leave the ground vegetation relatively intact, while more intense disturbances can result in the loss of all vegetation e.g., after volcanic activity or flooding (McKelvey 1963; Duncan 1993). Duncan (1993) found flooding to result in homogeneous deposits of silt across the forest floor which would have killed all the existing vegetation. The subsequent pattern of colonisation of the bare surface reflected seed dispersal mechanisms, species adaptations to different establishment sites, and stage of canopy closure. This contrasts to the present study, and others (e.g. Cullen 1987) where the ground layer (and possibly some of the understorey) vegetation remains relatively intact after the catastrophe. In such situations the

response to the canopy opening can come solely from the reorganisation of existing vegetation, or this can occur in conjunction with the establishment of new individuals. In North American forests a stands response to disturbance can come almost entirely from the release of subcanopy species (Veblen et al. 1989). In this present study it was unclear what proportion of response comes from reorganisation or new establishment, and the extent to which the reorganisation of existing vegetation may inhibit new establishment. Relatively little attention has been payed to these aspects for the southern hemisphere coniferous forests.

Stand S2

Patterns of stand development in canopy gaps are less predictable than after a catastrophe. For stand S2 different species established in different sized canopy openings. *Dacrydium*, *Prumnopitys* and *Phyllocladus* established in larger canopy openings while *Weinmannia* and *Quintinia* generally monopolised smaller canopy gaps. The exact size of gap that favoured one species over another was unclear, and may vary depending on the presence of advanced regeneration. Read & Hill (1988) found that in Tasmania, angiosperms could monopolise both small and large canopy gaps depending on how well they were represented in the understorey prior to disturbance. As a result regeneration of the conifer *Phyllocladus asplenifolius* often failed. If such competition was reduced *Phyllocladus* regeneration could occur in similar gap sizes to those previously monopolised by angiosperms. In this present study seedlings and saplings of *Weinmannia* and *Quintinia* were generally abundant across all three stands, however the extent to which they may exclude establishment of other species was unclear.

The dominance of *Dacrydium* across the stand reflected its success at colonising sporadic gaps. Studies have suggested that *Dacrydium* achieves canopy status by a gradual increase in height under an angiosperm canopy where light levels may be higher than under the canopy of associated conifers (Poole 1937; Six Dijkstra et al. 1985). If this was so it may be reflected in the age-diameter relationship. The age/diameter relationship for *Dacrydium* in stand S2 and for *Dacrydium* in Six

Dijkstra et al. (1985) indicated a less variable relationship up to c.170 years after which diameter was more variable for a given age. This may be the age at which some *Dacrydium* overtop subcanopy *Weinmannia* and *Quintinia*. A better relationship up to this point suggests *Dacrydium* trees continue to grow rather than remain suppressed under the canopy. This contrasts to *Libocedrus bidwillii* in sub-alpine *Nothofagus* forest where growth to maturity is achieved by successive periods of release and suppression following successive periods of canopy die-back of shorter lived generations of faster growing *Nothofagus* species (Ogden & Stewart 1995). Differences in growth rates between trees growing in shaded and open sites have also been shown for *Athrotaxis selaginoides* in Tasmania (Ogden 1985a). An ability to grow more quickly in open conditions may be a contributing factor to the success of the less shade tolerant conifers following a catastrophic disturbance. Faster height growth rates in open conditions would enable conifers to compete more effectively with associated angiosperms whose growth rates may not differ substantially to that in small canopy gaps.

This pattern of development to maturity for *Dacrydium* contrasts with that of *Prumnopitys*, whose age-diameter relationship suggested consistent height growth to maturity. This suggests *Prumnopitys* is less susceptible to changes in its environment once established. However this view is inconsistent with its preferential establishment in medium sized canopy openings, which reflects an establishment response to increased light levels. Elsewhere more shade tolerant conifers can regenerate under closed canopy conditions (Midgley 1992; Enright 1982a) and can show increased height growth to raised light levels, e.g. *Araucaria cunninghamii* in New Guinea (Enright 1982a). In the present study *Prumnopitys* seedlings/saplings showed no difference in height growth for saplings growing in shaded and open conditions (Chapter 3)

Regeneration of *Phyllocladus* was similarly limited beneath subcanopy and canopy trees. Growth to maturity also appeared limited as reflected by the paucity of stems of *Phyllocladus* >200 years. This may reflect an inability to compete effectively with associated species.

Regeneration of *Weinmannia* was also limited by subcanopy and canopy trees as reflected by the spatial patterns. However the gap regeneration characteristics and scales of clumping suggested that mature *Weinmannia* and *Quintinia* generally established in response to smaller canopy openings. June (1982) suggests such a pattern reflects greater shade tolerance. However certain life history characteristics can also account for this. Both *Weinmannia* and *Quintinia* can reiterate by suckering and layering, generally have high numbers of seedlings and saplings and have high light adaptiveness. The advantage of a high density of saplings/suckers can be explained in terms of Egler's (1954) initial floristic composition model or similarly Connell & Slatyer's (1977) inhibition model where the gap growing space is quickly pre-empted on account of the numbers and faster growth. The high juvenile numbers of seedlings and saplings of *Weinmannia* and *Quintinia* in all three stands is consistent with this theory.

High light adaptiveness enables *Weinmannia* and *Quintinia* to coexist under a closed canopy at a sapling stage with an ability for rapid height growth to increased light levels (Bigcas 1992). A fast height growth rate is important in small gaps where gap capture is a race between a trees rate of height growth and the growth of surrounding trees (Ogden et al. 1987).

Stand S3

Patterns of stand development in canopy gaps in stand S3 were similar to those in stand S2. However, establishment of *Weinmannia* was favoured in small canopy gaps over *Quintinia*. This could reflect underlying site differences between stands S2 and S3 associated with surface age. However, stems of *Quintinia* unlike *Weinmannia* were not clumped at large scales which suggests *Quintinia* establishment was more restricted to smaller, but patchily distributed establishment sites. These sites were not favoured by *Weinmannia* as small stems (young?) of both species were spatially segregated.

Seedling and sapling establishment patterns

The physical environment to which a seedling/sapling is subjected affects its probability of survival and recruitment into a population. Aspects of the physical and biotic environment form components of the plant habitat and regeneration niches defined by Grubb (1977). The physical and biotic environment changes as a stand ages. This reflects both the effects of disturbance and changes in stand structure. With stand age canopy structure changes, which has a pronounced influence on the spatial distribution of light within a forest (McDonald & Norton 1992) to which species differentially respond (Canham 1989). Disturbances similarly effect the distribution of light within a forest but also influence the availability of different establishment sites (pits, mounds, logs etc) upon which species differentially establish, e.g., uprooted trees create different opportunities for seedling establishment than snapped trees.

In this study stand structure varied between stands; associated with this were different understorey light environments as reflected by differences in the percentage of different canopy cover classes sampled within each stand. The different light environments were associated with differences in the relative abundance of seedlings. The highest number of seedlings of *Dacrydium* and *Lagarostrobos* were present across stand S1 where the light conditions were the highest, which in conjunction with their preferential establishment beneath more open cover classes reflects their less shade tolerant nature. The better light conditions across stand S1 relative to stands S2 and S3 may reflect a combination of a gradual opening of the canopy as self thinning progresses, crown architecture and canopy composition. Canopy trees modify the understorey light environment differentially according to canopy architecture and crown density. The crown form of *Dacrydium* trees can be quite variable depending on age and vigour. With age *Dacrydium* crowns become cylindrical or rounded until in emergent trees the crown is irregular with a few major branches supporting most of the foliage (Norton *et al.* 1988). The canopy of *Lagarostrobos* trees appeared less dense and generally had a pyramidal form while that of *Prumnopitys* was more dense and generally spread out horizontally creating dark understorey conditions (per obs). Both stand S2 and S3 possessed numerous mature *Prumnopitys* and many mature *Dacrydium* with heavily branched and spreading crowns. This was

reflected in the increased proportion of more closed canopy light conditions sampled and consequently fewer *Dacrydium* and *Lagarostrobos* seedlings occurred. *Dacrydium* and *Lagarostrobos* seedlings occurred least frequently beneath more closed canopy conditions compared to *Prumnopitys*. This is consistent with other studies who suggest *Prumnopitys* is more shade tolerant (Kell 1991; Lusk & Ogden 1992; Duncan 1993; Ogden & Stewart 1995).

Differences in stand structure can also effect competing ground vegetation. Where dense closed canopy conditions occur ground vegetation can be suppressed, so that conditions are more favourable for seedling establishment once a canopy gap is formed. A more open canopy may allow extensive development of ground and understorey vegetation so that gap formation primarily results in the reorganisation of existing vegetation through competition (Ehrenfeld 1980).

Many of the southern hemisphere conifers are considered less shade tolerant, however seedlings often establish beneath relatively intact canopies , e.g. *Dacrydium biforme* in montane *Libocedrus bidwillii* forest (Stewart & Rose 1989). However, in the present study seedlings that had established beneath closed canopies frequently occurred on raised substrates, as has been found elsewhere (Clayton-Greene 1977; Cullen 1987; Stewart & Rose 1989). *Lagarostrobos* and *Dacrydium* preferentially established on raised substrates, in all three stands. This may be a strategy to avoid competition from plants growing on the forest floor. If this theory is correct a greater proportion of seedlings may establish on level sites when bare surfaces are available for colonisation. This was found by Duncan (1993) for *Dacrydium* seedlings that colonised bare surfaces after flooding.

Although seedlings establishment may be common beneath forest canopies, the failure of such seedling banks to progress to a sapling stage is widely reflected in discontinuous age-class frequency distributions (Read & Hill 1988; Stewart & Rose 1989). *Dacrydium* and *Prumnopitys* seedlings that establish in low light intensities (beneath closed canopies?) have weak root systems (Cameron 1963; Kell 1991) which is likely to result in a reduced vigour and survival rate compared to seedlings that

have established under higher light intensities (gaps?). In some conifer forests seedlings establishment beneath a closed canopy is rare, while establishment is profuse in canopy gaps. e.g., in Tasmania *Athrotaxis selaginoides* seedlings occur at densities greater than 2000 ha^{-1} in canopy gaps (Read & Hill 1988).

Although seedling mortality may be high for conifers, at a certain height, size or age they can withstand lengthy periods of suppression. e.g., in this study *Dacrydium* saplings were found to be 105 years, while in montane *Libocedrus bidwillii* forests saplings may be as old as 200 years beneath closed canopies (Stewart & Rose 1989). In the Solomon Islands Whitmore (1966) found *Agathis macrophylla* seedlings to be 40 years at 30 cm height and saplings to be 75 years at 150cm height. This may reflect an adaption to long disturbance free periods.

The successful establishment of seedlings and growth to maturity is not just dependent upon the occurrence of canopy gaps or an ability to withstand lengthy periods of suppression. Successful establishment also relies upon the coincidence of a suitable establishment site with a canopy opening. Seedlings generally establish preferentially on different substrates or microtopography positions. Duncan (1993) found seedlings to partition establishment sites according to the microtopography reflecting tolerance to differences in soil drainage. *Dacrydium* established on level sites while *Weinmannia racemosa* and *Prumnopitys* established on better drained raised sites. In this study *Dacrydium*, *Lagarostrobos* and *Prumnopitys* all preferentially established on raised sites, in particular *Dacrydium* and *Lagarostrobos* in stand S1. This could reflect poor soil drainage. However, seedlings that establish on raised sites can be ephemeral due to the poor water holding capacity of some raised establishment sites e.g., logs (Wardle 1991). However, Salltwater forest rarely has dry spells longer than fifteen days, so this may not be a problem.

Although, *Prumnopitys* was more frequently found on raised sites a higher percentage occurred on the forest floor compared to *Dacrydium* and *Lagarostrobos* which is inconsistent with other studies

where raised sites were favoured (Collins 1986; Duncan 1993). The distribution may simply reflect an ability to withstand more shaded conditions, and does not necessarily reflect a site where a seedling will grow into a mature tree.

For *Weinmannia*, *Quintinia* and *Phyllocladus* seedling distributions generally reflected the abundance of different substrate types, however saplings of *Quintinia* favoured raised sites suggesting a preference for better drainage. The lack of preference for *Weinmannia* saplings may simply reflect extensive suckering and layering contributing to a higher count on the forest floor. This contrasts to beech\angiosperm forest in Fiordland where *Weinmannia* establishes solely on raised sites. Epiphytic establishment on tree fern trunks can also be important for successful establishment of Weinmannia (Veblen & Stewart 1982), however large tree ferns were generally uncommon in the stands S1, S2 and S3.

The pattern of seedling establishment on different substrates suggested a general trend of decreasing preference for raised establishment sites from, *Dacrydium* and *Lagarostrobos*, to *Quintinia* and *Weinmannia* with *Prumnopitys* and *Phyllocladus* least likely to establish on raised sites. This distribution suggests that species do not partition establishment sites in relation to substrate type to the extent that occurs in other New Zealand forest types (Stewart 1986; Duncan 1993).

The above establishment patterns occurred in forest stands that have a significant history of disturbance. However, some southern hemisphere conifer forest types are apparently stable and seedling and saplings establish in the absence of any major canopy openings. In such forests the most shade tolerant conifers occur and regenerate continuously. Midgley et al. (1990) provided evidence of continuous regeneration of *Podocarpos falcatus* and *Podocarpos latifolius* in the Southern Cape forests of South Africa where only small canopy gaps occurred, formed by standing dead and snapped trees (Geldenhuys & Maliepaard 1983). The ability of these conifers to regenerate under closed canopy condition was reflected in the spatial distribution and patterns of

association of saplings. Both Midgley et al. (1990) for *Podocarpos latifolius* and *Podocarpos falcatus* in South Africa and Enright (1982a) for *Araucaria cunninghamii* in New Guinea found that saplings of these shade tolerant species were not associated with conspecific adults or canopy gaps. This implied that they could regenerate both in canopy gaps and under closed canopy conditions adjacent to adult trees (parents?). By contrast, Enright (1982a) found the less shade tolerant *Araucaria hunsteinii* to be spatially segregated from parent trees and was found in groups attributed to establishment in canopy openings. In this study saplings of *Dacrydium* (less shade tolerant) and *Prumnopitys* (more shade tolerant) showed patterns more typical of less shade tolerant species, although *Prumnopitys* had established in smaller groups which may reflect an ability to establish in smaller canopy openings.

Such spatial patterning of saplings for species that rely on gap formation for regeneration may not always be evident. Less shade tolerant species can regenerate continuously without canopy disturbance, but such a regeneration pattern is restricted to more open forest types, e.g., *Athrotaxis selaginoides* in Tasmania (Read & Hill 1988) or where poor nutrient status of soils has reduced the stature of associated species, e.g., *Phyllocladus alpinus* in the montane forest in New Zealand (Veblen & Stewart 1982).

These seedling and sapling patterns show the effect of stand structure, canopy gaps and substrate on establishment. However, what combination of these factors favours successful growth to maturity for a particular species is unclear.

6.4.4 Main factors affecting forest composition

Effects of different disturbance histories

When gap processes differ, floristic composition also differs (Brokaw & Scheiner 1989), with maximum species richness occurring at intermediate levels of disturbance (Connell 1979). The effect of differences in disturbance history on forest composition reflects the non-equilibrium view point

(reviewed in chapter 1) where recurrent disturbances prevent competitive equilibrium being attained, and are the source of much of the environmental heterogeneity to which species differentially respond (Pickett 1980). Here differences in stand composition are explained in relation to the different spatial and temporal patterns of disturbance that have affected the stands S1, S2 and S3.

Differences in the spread of ages for the conifers and the preferential establishment of seedlings beneath different overhead canopy cover classes suggests that the conifers have different light requirements, partitioning establishment sites to an extent according to different stages of canopy closure/size of canopy opening. Differences suggested that *Lagarostrobos colensoi* and *Phyllocladus alpinus* were the least shade tolerant followed by *Dacrydium cupressinum*, with *Prumnopitys ferruginea* the most shade tolerant. This implies species preferentially establish in different size canopy openings.

In stand S1 where the largest but least frequent disturbance had occurred stand composition can be attributed to massive establishment (or massive recruitment of an established seedling bank) of the less shade tolerant species, *Lagarostrobos*, *Dacrydium* and *Phyllocladus*. Although in stand S1 *Phyllocladus* was not represented as a tree, it was evident from the population structure of the regenerating stand S1r (sampled as representative of an early developmental stage of stand S1) that it does regenerate contemporaneously in large numbers with *Dacrydium* in large openings. *Prumnopitys stems* had not established in such numbers and were uncommon compared to *Dacrydium* and *Lagarostrobos*. This may partly be due to the reduced competitive ability of *Prumnopitys* seedlings on such poorly drained soils (Section 6.3.2), particularly when seedlings of *Prumnopitys* predominantly established on the forest floor. Alternatively the paucity of established stems could reflect a past period of high stem mortality. *Prumnopitys stems* may be more susceptible to stress and subsequent mortality on such a poorly drained site compared to associated species.

In addition to the scale of disturbance, frequency of disturbance is also critical to the explanation of

stand compositional trends. For stand S1 the absence of recurrent disturbances accounts for the ongoing compositional shifts in the stand. *Phyllocladus* stems, once abundant have now died out, and similarly the *Lagarostrobos* component is decreasing in proportion as indicated by the number of dead stems. These changes can be explained by interspecific competition caused by the competitive dominance of *Dacrydium*. As stems of *Dacrydium* overtop other species, light resources will become limiting. Furthermore, if the time interval between successive canopy openings suitable for a species regeneration is greater than its life span, or is greater than the time in which it will succumb to the effects of competition, the species will become locally extinct. These ongoing successional changes, in the absence of further significant canopy openings prevent stands from reaching compositional equilibrium. This pattern of stand development reflects stand uniformity and is consistent with the sequence outlined by Six Dijkstra et al. (1985) where compositional and structural differences across the terrace forest were primarily attributed to stand age.

For stand S2, compositional equilibrium is likely to be maintained by the recurrent smaller scale disturbances that have occurred. Recurrent disturbances have created a more heterogeneous environment as reflected by the less uniform stand structure compared to stands S1 and S2, allowing the coexistence of species with varying degrees of competitive ability. Disturbance has occurred at a sufficiently high frequency to maintain recruitment of the less competitive *Phyllocladus* and *Lagarostrobos*. The occurrence of recurrent small gaps has favoured regeneration of *Prumnopitys* on account of its ability to maintain height growth once established, despite canopy closure (see Section 6.22).

For stand S3 gap processes have been intermediate between stands S1 and S2, with recurrent disturbances from progressive canopy collapse occurring over a prolonged period (c.300 years). Recurrent disturbances over this period account for the high proportion of *Prumnopitys* stems. However, recruitment of *Dacrydium* and *Lagarostrobos* declined over the last c. 250 years reflecting a long relatively disturbance free period. This accounts for the paucity of regeneration of

Phyllocladus and *Lagarostrobos*, while the scarcity of mature stems of these species reflects competitive effects as in stand S1.

Weinmannia and *Quintinia* preferentially regenerated in response to smaller sized canopy openings in all three stands (Section 6.2.2). An increase in the frequency of small canopy gaps is likely to shift composition towards an increased *Weinmannia* and *Quintinia* component. In addition a high frequency of disturbance favours species with shorter life cycles. Ogden & Stewart (1995) suggest mean longevities of New Zealand conifers and associated shorter lived angiosperms can differ by as much as 40%. A shorter life cycle for angiosperms is generally correlated with a shorter age to sexual maturity (Loehle 1987), which together with a propensity for suckering and layering confers a competitive advantage in forests that are more frequently disturbed. For conifer species age is not a good predictor of sexual maturity (Loehle 1987). However, New Zealand conifers are long lived and have slow growth, so their age to reproductive maturity could be much greater than associated angiosperms. Therefore with an increased frequency of disturbance such long lived species are more prone to local extinction. This compares to the situation in montane environments in New Zealand where frequent disturbance occurs from mass movement on the steeper ground favouring relatively short lived seral species (Stewart & Harrison 1987). The composition of stand S2 where the basal area of *Dacrydium* was at its lowest compared to the angiosperms is consistent with this theory.

One of the components of the non-equilibrium theory is that patches (gaps) must be distributed such that they can be colonised by poorer competitors (Pickett 1980). This implies that if a stand devastating disturbance occurs which removes all parent trees the subsequent pattern of colonisation will depend upon the seed dispersal mechanisms for non-suckering species, and their proximity to the disturbed site. All the conifers have bird dispersed seed (Beveridge 1964), although *Dacrydium* has limited wind dispersal capabilities, generally up to ten metres from the parent trees (Norton et al., 1988). However, there are important differences between *Dacrydium* and *Prumnopitys* seed

dispersal. *Prumnopitys* fruit are much larger and are limited to dispersal by larger birds such as keruru. *Dacrydium* fruit can be dispersed by a much wider range of birds but has a propensity for mast seeding (Norton & Kelley 1988) unlike *Prumnopitys* which can produce seed all year round (Brockie 1992). Hence time of gap creation in relation to seed production may also be important for *Dacrydium* establishment.

The presence of fewer *Prumnopitys* seed sources across terrace 1 (as reflected by the community composition) compared to the other conifers, and the more limited seed dispersal mechanism could limit the colonisation rate of a massively disturbed area. In addition, other studies have shown that *Prumnopitys* seedlings frequently establish near suitable bird perches (Kell 1991; Norton 1991; Lusk & Ogden 1992). The absence of such perches in a massively disturbed stand would confine establishment to gap edges. Hence a compositional gradient would be expected from gap edge to the centre reflecting ease of seed dispersal and time of seed production, and the relative abundance of parent trees in the surrounding forest mosaic. However, the catastrophically disturbed stand S1 appeared to be part of a larger patch so it is difficult to assess whether the above theory can explain aspects of the species distributions for this stand. A study of seed dispersal for different species from intact forest into logging clearings would be useful here.

For forest on terrace 2 and terrace 3, if a stand devastating disturbance occurred the gap may not necessarily be colonised by less shade tolerant species to the extent stand S1 has, because of the greater abundance of *Prumnopitys* parent trees in the adjacent forest. This highlights another important factor in determining future stand composition, that of the stand structure and composition at the time of disturbance. If the stage of canopy closure/distribution of gaps across the stand has enabled a substantial seedling bank to establish as for *Dacrydium* and *Lagarostrobos* in stand S1 and *Prumnopitys* in stands S2 and S3 the future canopy composition may largely be a function of the initial floristic composition (Egler 1954). Hence for stands S2 and S3 if a catastrophic disturbance occurred greater recruitment of *Prumnopitys* may occur from the seedling bank, resulting in an

increased relative abundance in mature forest compared to stand S1. The population structure of the large heavily disturbed gap on terrace 3 was consistent with this theory.

Terrace soils and their effect on forest composition

Terrace sequences of increasing age are commonly reflected by soil development and vegetation change. With time (100s-1000s of years) soils become increasingly well developed reflecting the influence of climate, vegetation, topography and parent material. Soil development results in increased depth, lower fertility and poor drainage. In south Westland soil development is strongly influenced by rainfall and site drainage (Smith & Lee 1984). In particular high rainfall, which promotes the leaching of soluble weathering products from the soils. The higher the rainfall, the greater the leaching loss and the faster the rate of soil development (Tonkin et al. 1985).

Organic and gley-podzols predominated across the terraces indicating that the soils were well developed. Podzolisation and gleying are common features of soils in the high rainfall areas of Westland (Sowden 1986). Podzol formation can occur within 150 years on freely drained sites and can promote the formation of gleyed soils. With podzolisation poorly permiable iron rich horizons can develop which can support perched water tables promoting waterlogging and subsequently gleying.

Differences in soils were apparent between stands S1, S2 and S3 reflecting a secular trend in soil development. The deepest and most poorly drained soils occurred across stand S1 on the oldest terrace and the shallowest and less poorly drained across stand S3 on the youngest terrace. These differences in stage of soil development are consistent with other studies on lowland forest sequences in Westland where poor drainage and increased soil depth are associated with landform age (Smith & Lee 1984; Sowden 1986).

The mechanism by which these soils are likely to increase in depth involves increased weathering of the parent material, increased loess deposits and increased accumulation of organic matter

(P.Almond pers comm). For soils in stand S1 organic horizons were frequently 1m or greater in depth reflecting a lengthy period of accumulation, and the failure of this material to breakdown due to the anaerobic conditions. In addition, differences in drainage between the stands may reflect differences in gradient, with terrace 1 possessing the least slope which would decrease the rate of run-off.

Forest composition was partly associated with the distribution of differently drained soils across the terraces. *Lagarostrobos* appeared to favour the most poorly drained soils reflected by its abundance in stand S1, 1.7 and 3.2. This has also been commented upon by Wardle (1977), Smith & Lee (1984), Wardle 1991, Norton & Leathwick (1990) and Ogden & Stewart (1995), although its distribution has not been extensively studied. *Prumnopitys* was more abundant in the less poorly drained stands S2 and S3. The distribution of *Prumnopitys* is consistent with that observed by Collins (1986) who found *Prumnopitys* to increase in abundance from the poorly drained terraces to better drained sloping ground.

In addition, spatially segregated species distributions across stands S2 and S3 coincided to an extent with the distribution of differently drained soils, such that *Prumnopitys* favoured the less poorly drained soils in stand S3 and *Phyllocladus* favoured the most poorly drained soils in stand S2. Relatively minor differences in aerobic depth (soil drainage) have been related to significant differences in the distribution of plants in near by Ianthe Forest. Norton (1994) found differences of 5-10cm in aerobic depth to cause substantial differences in the relative abundance of the ferns *Blechnum discolor* and *Blechnum procerum*. The aerobic depth of stands S2 and S3 differed from stand S1 by c. 10cm and 8cm respectively. The water table of stand S1 was almost uniformly at the surface which is likely to limit the distribution of plants that preferentially establish on the forest floor.

Vegetation change associated with Westland soils has been investigated by many, however most studies have focused on vegetation, soil, landform and topographic relationships highlighting more

major floristic differences, from mountain to flood plane and from steep sites to level sites (Chavasse 1971, Stewart & Harrison 1987; Norton & Leathwick 1990; Duncan et al. 1991). This contrasts to this present study where floristic differences occurred across the one landform type.

Variation in composition within stands and between stands on the same terrace associated with differently drained soils can not be explained in terms of a secular trend of soil development. The variation in soil drainage found within terraces as was evident between stands S1 and 1.4 on terrace 1 and S3 and 3.2 on terrace 3, and within stands S2 and S3 could reflect differences in the soil development process. The meltwater of the glacial advances forming the terraces would have created a system of deep channels and raised sand bars similar to those formed by the nearby Poerua river. Organic matter would accumulate in the channels cut by the meltwater, promoting ponding and the formation of very poorly drained organic soils. A similar explanation accounted for the floristic variation across mire-forest ecotones in south Westland (Norton 1989) and across more recent river terraces (Smith & Lee 1984). Mires occur on deep peats reflecting the presence of old river channels. Vegetation changes across mires parallel the change in peat depth away from the river channel centre reflecting decreasing wetness until forest vegetation occurs (Norton 1989). Smith & Lee (1984) also found soil drainage to vary for forest that had established on river terraces. They found anomalous distributions of *Lagarostrobos* on the freely drained terraces to reflect the accumulation of peat which had filled in old scour channels resulting in poorly drained sites. Hence heterogeneity in the soil drainage pattern across the terraces in the present study may in part account for the complex of *Dacrydium* dominated forest communities found across the terraces.

For stable landforms such as the glacial terraces in Saltwater Forest, soil development has proceeded unaffected by major disturbance for long periods (Basher 1986; Stewart & Harrison 1987), although some redirection of soil development can occur from pits and mounds associated with uprooted trees (Adams & Norton 1991). Pits and mounds create poorly and well drained sites respectively. Such variation could account for anomalous plant distributions within stands.

However, differences in soil development and soil drainage *per se* are only partly responsible for differences in stand composition. It appears that differences in soil drainage and terrace age are not sufficient or varied enough to explain the substantial differences in the relative abundance of conifers between stands, and differences in species richness between the five different communities identified across the terraces (Chapter 4). The overriding influence on forest composition between the terraces appears to be differences in disturbance history.

6.4 5 Main factors causing variation in the effects of disturbance

Variation in the effects of disturbance associated with soil drainage

For other southern hemisphere coniferous forests catastrophic to gap-phase patterns of regeneration have primarily been attributed to different types of disturbance e.g., volcanism, mass-movement, flooding, fire and windthrow (Veblen & Lorenz 1987; Duncan 1993; Read & Hill 1988). This reflects variation in the stability of the environment associated with different frequencies and scales of exogenous disturbance phenomena. Veblen et al. (1992) showed that the effects of different disturbance types can vary along a major environmental gradient associated with landform changes and different forest types across the Andes, from the flat plains to rolling foothills and to the high mountains. However, in this study the effects of one disturbance type (presumed to be windstorms) varied across the same landform and forest type according to the distribution of very poorly and poorly drained soils, reflecting differences in stand stability. In this study stand stability appeared to be affected by soil drainage, soil depth, rooting characteristics and stand structure.

Previous studies in Saltwater forest have suggested that differences in soil drainage are associated with different patterns of windthrow, between the hill and terrace forest (Simmons 1982). The likelihood of trees being windthrown relates to the physical conditions of the soil and the depth and extent of rooting of individual trees or stands, which will ultimately determine whether or not windthrow will occur (Fraser 1962). Trees growing in wet soils such as gleyed and organic soils are more likely to be uprooted than those growing on better drained sites (Smith & Watts 1987; Schaetzl

et al. 1988). Trees growing on such soils are generally shallow rooted, which in combination with a decreased soil shear strength increases susceptibility to windthrow. In addition, roots growing in wet soils have an increased incidence of root rot which can markedly reduce a trees resistance to windthrow (Fraser 1962).

However, in this present study *Dacrydium* trees growing on the most poorly drained organic soils were not shallow rooted since structural roots were evident throughout the poorly drained organic horizons (per obs). Simmons (1982) found roots of *Dacrydium* to penetrate up to 1.7m on similarly drained soils in the same forest, while on less poorly drained soils root depth was limited but lateral growth was greater creating a more stable base. Such root plates can be up to 20m wide for large trees on less poorly drained soils, while trees of a comparable diameter on the most poorly drained soils can have smaller root plates of only 8-10m across. Simmons suggests such differences account for different patterns of windthrow between poorly drained terraces where uprooting was common and better drained sloping sites where snapped trees were common. Although *Dacrydium* trees growing on the most poorly drained soils in this study were deeply rooted, the fluid nature of the organic soils would result in a low shear strength increasing the risk of windthrow compared to the less poorly drained mineral soils.

Such rooting patterns contrast to those reviewed by Schaetzl et al. (1988) where tree rooting in poorly drained soils was generally restricted to the surface aerobic horizons, increasing the risk of windthrow. However, they suggest tree rooting characteristics vary between genus affecting resistance to windthrow. Here the treefall characteristics suggested that angiosperms were more commonly uprooted than snapped, while *Lagarostrobos* primarily died standing. This may reflect differences in root architecture and differences in the resistance of roots to decay.

Differences in stand stability between trees growing on the very poorly drained soils (e.g. stand S1) and the less poorly drained soils (e.g. stand S2) partly accounts for the contrasting disturbance

histories. On the most poorly drained deep organic soils catastrophic disturbance had occurred as for stands S1, 1.7 (terrace 1), while on the less poorly drained mineral soils in stands S2 and S3 smaller disturbances predominated. Stand stability is also affected by soil type in montane *Libocedrus bidwillii* forests where stand stability is reduced by shallow soils overlaying hard iron pans, resulting in more frequent small scale windthrows (Veblen & Stewart 1982).

In addition to differences in scale of disturbance, the mechanism by which windstorms cause windthrow can also vary. Wind can throw a tree in one of two ways. The first is simply for a gust of wind to have sufficient speed or duration that a tree's critical turning moment is exceeded. This most likely explains the mechanism by which catastrophic disturbance occurs. The second mechanism is when the wind is not so strong but is sufficient to start the tree oscillating. If the wind continues the oscillations get bigger such that the critical turning moment at the base is exceeded and windthrow occurs (Smith et al. 1987). Oscillation of tall *Dacrydium* trees was a frequent occurrence on windy days (pers obs) and may account for much of the windthrow of single large stems. Exposure, slope and elevation are also important variables in the determination of windthrow potential (Schaelzt et al. 1988), however these factors were not influential in the present study.

In other studies on the effects of disturbance a single forest type has been found to experience a range of different disturbance types which account for variation in the frequency and scale of gap formation. e.g., for *Athrotaxis selaginoides* forest in Tasmania wildfire and single treefalls create different scales and frequencies of canopy openings (Cullen 1987), while in montane *Libocedrus bidwillii* forest in New Zealand windthrow and mass movement are important (Stewart & Rose 1989). In Chile volcanism and windthrow effect *Araucaria araucana* forest types (Veblen 1982).

The influence of stand age and canopy structure on the effects of disturbance

In addition to differences in soil drainage, stand age and canopy structure can have significant effects on the susceptibility of a stand to disturbance. Foster (1988) found wind damage exhibited an

approximately linear response with stand age, explained by the progressive changes that occurred in tree structure and architecture. With increasing age greater tree height and canopy size induce greater susceptibility to windthrow (Wilson & Archer 1979). Furthermore, with increasing stand age trees are increasingly likely to suffer from root rot and or heart rot predisposing them to windthrow.

For more even canopied stands such as for stand S1, although having established on the most windthrow prone poorly drained soils, the susceptibility to windthrow will at present be reduced due to the high stem density. A high stem density affords a degree of stand stability. Stand stability increases with stand density owing to the greater ability of dense stands to dissipate incoming winds because of the damping effect of neighbours, and the added stability of interlocking root systems (Smith & Watts 1987). However, with increasing stratification and differentiation with age, the increase in canopy surface roughness (Kelty 1984) facilitates wind turbulence, increasing the likelihood of blowdowns (Savill 1983), and the structure may tend towards that of the more sporadically disturbed stand S2 where the stand had a less even canopy. There may also be differences in response to disturbance between open-grown trees and dense stands of trees such as those that establish after a catastrophic disturbance. Open grown trees develop a sturdier root system in response to wind pressure and growth (Wilson & Archer 1979) reducing susceptibility to windthrow.

In the absence of further catastrophic disturbance stand structures will tend to an all-aged structure, as stands age sporadic gaps will form resulting in gap-phase regeneration. An increase in the frequency of catastrophic disturbance will promote more synchronous regeneration across the most poorly drained terraces and uniformity in structure amongst stands. Whether stands on the less poorly drained sites succumb to catastrophic disturbance, may depend on stand age and the intensity of the disturbance.

6.4.6 Other factors contributing to forest variation

Variation in the effects of disturbance appeared to be the main factor accounting for differences in stand composition and compositional shifts, however in long disturbance free periods other factors account for forest variation and can modify a stands response to disturbance. Forest variation attributed to species interactions can be important, mechanisms of which have been summarised by Connell & Slatyer (1977) (reviewed in Chapter 1). Vegetation change from species interactions results from the effects of particular species on another, either directly or through environmental modification (Veblen 1992) and can explain compositional shifts and alternation between species (Fox 1977). In this study interspecific competition accounted for ongoing compositional and structural changes. For stand S1 Interspecific competition favoured *Dacrydium* which had a competitive advantage over associated species, growing taller and having greater longevity. However interspecific competition in stands can be unimportant compared to intraspecific competition. Duncan (1993) found that interspecific competition to dominate in mixed species where *Dacrydium cupressinum* and *Dacrycarpus dacrydiodes* were spatially segregated to such an extent that species interactions were minimal. As stands age and less competitive species become locally extinct, such as *Phyllocladus* and *Lagarostrobos* in stand S1 intraspecific competition will become increasingly important.

The competitive dominance of one species over another can be modified by the differential effects of site on species growth rates. Webb & Tracey (1967) and Midgley & Bond (1989) suggest angiosperms exclude conifers to all but the most marginal sites due to their faster growth rates. In this present study the angiosperms *Weinmannia* and *Quintinia* may have depressed growth rates on the most poorly drained soils such as were found across stand S1. This would allow conifers to compete more effectively and may contribute to the success of catastrophic regeneration of *Dacrydium* across stand S1.

Species interactions attributed to habitat and regeneration niche modification by canopy trees has

partly been discussed (Sections 6.2.3). Canopy trees can also directly modify the understorey environment through the accumulation of litter and leaching of leaf exudates, and indirectly through the response of understorey plants. The effects of such modification can prevent germination and growth of the understorey plants. e.g., leaf litter can smother seedlings while the leaf exudates from conifer foliage has strong allelopathic effects on seed germination and seedling growth (Brockie 1992). The negative association between *Prumnopitys* trees and saplings of *Dacrydium* may reflect such factors increasing the probability of replacement by another species.

Indirect species interactions can also account for spatial patterns , e.g. the distribution of *Prumnopitys* saplings has been associated with the behaviour of birds, which disperse the fleshy seed as has been discussed. Saplings of *Prumnopitys* have been associated with large angiosperms in other conifer forests reflecting their use as bird perches (Norton 1992; Lusk & Ogden 1992). In stand S3 the establishment of small (young?) *Weinmannia* away from large (old?) *Weinmannia* may be related to the avoidance of species specific pathogens, such that the establishment sites were colonised by small *Quintinia*. This parent juvenile avoidance strategy enables greater niche differentiation, and may also avoid interspecific competition between establishing species in some instances.

However, Read & Hill (1988) argue that such autogenic mechanisms of vegetation change are of secondary importance in determining future canopy composition because of the slow rate at which they operate in relation to the frequency of large scale disturbances. Here the contribution such autogenic factors will make towards vegetation change is likely to be more prominent when combined with the influence gaps. Species interactions may determine whether a species survives on a particular establishment with successful regeneration reliant upon the coincidence of a suitable canopy opening.

Chapter 7

Concluding Discussion

Forest variation (stand structure and composition) was primarily associated with terrace age. This variation reflected both the influence of stage of soil development/soil drainage and disturbance history. Not only were the relative effects of both these factors superimposed but the effects of disturbance varied according to stage of soil development/soil drainage. Very poor soil drainage and the associated catastrophic disturbance favoured establishment of *Lagarostrobos colensoi*, while less poorly drained sites where more frequent canopy gaps were formed favoured regeneration of *Prumnopitys ferruginea.* In addition stand composition was affected by stand structure. Where stands were most uniform, such as had established after a catastrophic disturbance species richness was lower.

Although the separate effects of such environmental and disturbance factors on forest variation have been documented before, this present study differed because environmental variation and variation in the effects of disturbance reflected secular changes over millennia. This has important implications for the long term stand dynamics of the terrace forest.

As the terrace soils age, soils increase in depth and soil drainage decreases. Provided the frequency of intense windstorms remains relatively constant, the probability that stands on the less poorly drained soils across terraces 2 and 3 will be catastrophically disturbed will increase over millennia. This will be reflected by more contemporaneous stand establishment across all the terraces, and a compositional shift towards less shade tolerant conifers, a reduced angiosperm component and reduced species richness.

Structural and compositional shifts envisaged in this secular model have been explained by Six

Dijkstra et al. (1985) as reflecting different stages in one stand development sequence (reviewed in Chapter 5). However Ogden & Stewart (1995) recognised similar changes in their generalised "lozenge" model of periodic regeneration for Westland forests. The "lozenge" model, adapted from the "cohort regeneration" model for *Agathis australis* (Ogden 1987) depicts a secular change (over a few generations) in successive patterns of stand development associated with changes in the disturbance regime. The process is initiated by large scale disturbance resulting in relatively synchronous regeneration of the dominant conifers. With increasing stand age self-thinning occurs predisposing the stand to secondary disturbances. Gap-phase regeneration follows resulting in successively less synchronous and less dense waves of regeneration.

Differences in stand structure between stands S1, S2 and S3 reflect different stages of such a model, with the uniform even-aged stand S1 representing the initial catastrophic regeneration, followed by stand S3 where most regeneration of *Dacrydium* occurred over a restricted period, but from overlapping gap formation episodes. The final stage is represented by stand S2 where the all-aged and over-lapping age-group structure has arisen from recurrent gap formation episodes. Whether a stand will develop the predominantly gap-phase regeneration pattern associated with later stages of the lozenge model will depend on site stability and the frequency of major disturbances. The secular change in the disturbance regime envisaged in the "lozenge" model may be reset more frequently or progress at different rates on sites of poor drainage. In a disturbance prone environment the more advanced stages of stand development may never be attained due to repeated large scale disturbance, so that even-aged, uniform stands predominate.

The findings of this thesis differed from others on the stand dynamics of southern hemisphere coniferous forests on two accounts. Firstly the effects of one disturbance type varied along an environmental gradient over one forest type which explained changes in stand structure and composition across terrace forest. Veblen (1992) also showed the effects of various disturbance types to be linked to environmental gradients, however his study focused on landscape-scale variation across different forest types. Secondly this thesis has shown that changes in the stand

dynamics of the terrace forest occurs over millennia (reflecting landform age) affecting stand structure and composition, reflecting equally long term soil development. These findings suggest future studies on forest stand dynamics should consider landform age, and associated environment/disturbance interactions, as this can account for a significant part of stand structure and compositional variation between identical landforms.

Chapter 8

Summary of main findings

1. Errors from ageing trees using increment cores, associated with the time taken to reach coring height for species growing in well lit and shaded environments, and due to non circuit uniformity suggest 50 year age-classes are suitable intervals for making realistic comparisons of age-class frequency distributions.

2. Stands across the three differently aged glacial terraces varied in composition and species richness, however one community type was dominant on each terrace. A floristic gradient occurred across the terrace forest which was interpreted as reflecting variation in edaphic conditions associated with terrace age, together with differences in stand structure.

3. Stand structures were highly variable within and between terraces. This appeared to reflect a combination of stands at different stages of development, and different patterns of stand development reflecting different disturbance histories. The different stand structures differed in composition reflecting the different community types across the terraces.

4. The dominant stand on each of the differently aged terraces differed in structure and composition. This stand variation was associated with different disturbance histories. Catastrophic disturbance, recurrent gap formation and progressive canopy mortality had occurred across the stands on the old, middle and youngest terrace respectively.

5. The different disturbance histories were associated with different canopy cover light environments which affected the distribution and abundance of seedlings. Seedling distributions were also determined by preferential establishment on different substrates.

6. Differences in composition for the main stands primarily reflected the effect of different scales and frequencies of disturbance, and to a lesser extent stand age and species preference for differently drained soils

7. Differences in soil profile and soil drainage characteristics between stands on the differently aged glacial terraces reflected a secular trend in soil development from shallow less poorly drained mineral soils, to deeper more poorly drained organic soils.

8. The effects of disturbance varied according to the distribution of differently drained soils. On the most poorly drained organic soils catastrophic disturbance had occurred, while on less poorly drained soils recurrent gap formation had occurred. These differences were presumed to reflect differences in stand stability, however stand age and canopy structure were also considered to significantly affect the susceptibility of a stand to disturbance.

9. A secular change in the stand dynamics of terrace forest is envisaged over millennia reflecting soil development. This accounts for variation in stand structure and composition between differently aged glacial terraces in Saltwater Forest.

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